GENETIC VARIATION IN NUTRIENT ABSORPTION IN SLASH PINE

By

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TO

MY WIFE

PAULA ALICE JAHROMI

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GENETIC VARIATION IN NUTRIENT ABSORPTION IN SLASH PINE

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Chairman: Ray E. Goddard
Major Department: Agronomy

In a replicated N-P factorial experiment, 240 control-pollinated progenies of slash pine (Pinus elliottii var. elliottii Engelm.), were grown for a period of 25 months. The progenies consisted of 5 female parents crossed with 5 male parents in a balanced incomplete factorial design. There were 20 crosses, each represented by 12 full-sibs in the experiment.

Data were analyzed for N and P absorption, translocation, tissue content, and growth characteristics. In a few traits, the effects of male or female parents were significant. However, the female x male interactions (mostly due to nonadditive genetic factors) were highly significant for all traits. There were also highly significant effects of female x fertilizer treatment, male x fertilizer treatment, and female x male x fertilizer treatment interactions. Such interactions were evidence of differential response of slash pine to fertilizers. Parents influenced the response of their progenies to fertilizer treatments to a great extent. Responses to fertilizer treatments varied in different specific crosses.

The fertilizer treatments, regardless of genetic effects and genotype x fertilizer treatment interaction, had great effects on growth response and tissue content of progenies. Except for height growth, which was maximum under P treatment, the progenies produced maximum wood and foliage under NP treatment.

Heritability estimates were made for N and P absorption, translocation, tissue content of plant portions, and growth characteristics. For each trait, heritability was estimated for general and local adaptability. Heritability values for N and P absorption were 0.197 and 0.231, respectively, for general adaptability and 0.734 and 0.678 for local adaptability. Slightly lower values were obtained for N and P translocation. Inheritance of height growth was strongest of traits studied with heritability values of 0.314 and 0.740 for general and local adaptability, respectively.

Absorption, translocation, and needle content were genetically correlated with growth characteristics. Genetic correlation between N absorption and height growth was 1.07. Slightly higher correlations were found between translocation and height growth. Genetic correlations between absorption, translocation and needle content and diameter growth were not significant. It was assumed that significant correlations between these traits were due to pleiotropic action of genes.

In a supplementary experiment using ^{33}P and open-pollinated progenies of the female parents used in the control-pollinated experiment, the incorporation of phosphate into acid-soluble, nucleic acid,and phospholipid-phosphoprotein fractions was studied. The seedlings were grown for a period of 4 months under 5 combinations of N and P. Data showed that (a) incorporation of phosphate into these fractions was highly affected by the rate of N and P in substrate, (b) incorporation of phosphate into different fractions in seedlings treated with 50 ppm of N and 5 ppm of P (optimum treatment) was highly associated with height growth and top fresh weight, (c) there were significant correlations between incorporation of phosphate into nucleic acid or phospholipid-phosphoprotein fractions in roots and growth, when averaged values over all fertilizer treatments were used, and (d) there were significant correlations between acid-soluble phosphate in terminal cm shoots and growth characteristics. The ranking of lines for incorporation and growth was in agreement with ranking of general combining ability of these lines used in control-pollinated experiment.

The results of experiments suggest that genetic variation in rate of growth is related in part to genetic variations in nutrient absorption and translocation. Substantial improvement of slash pine growth on certain nutrient deficient soils may be possible by planting fertilizer-responsive genotypes selected for the soil condition in conjunction with supplemental fertilization. Much greater improvement should be obtained if procedures can be developed to take advantage of high specific combining ability for nutrient response.

INTRODUCTION

Forest fertilization is now in use both on a commercial scale and in research programs. In 1969, approximately 35,000 acres of young pine plantations were fertilized in the Coastal Plains (Anonymous, 1970). This acreage was expanded at a rapid pace so that in 1970 about 175,000 acres of forests had been supplied with fertilizers (Anonymous, 1971).

Soils of the Coastal Plains vary greatly in their inherent fertility and in their need for fertilizers. Undoubtedly, this is the case for other regions as well. Thus, in each area fertilization must be practiced according to the needs of that area. Moreover, tests have shown that slash pine families differ greatly in their capacity to grow under different fertilizer regimes and in their responsiveness to fertilizers. Tests have shown that these characteristics are genetically controlled. Therefore, there is a potential for breeding slash pines with the capacity to especially benefit from fertilization for high wood volume production. Thus, knowledge of the heritability of nutrient absorption and magnitude of genotype x fertilizer interaction is of fundamental importance in planning programs and in predicting genetic gain.

The existence of strong genotype x fertilizer interaction necessitates the evaluation of response of progenies of different families under a variety of soil nutrients similar to those on which the progenies will ultimately be planted. The information gained may be used to specify fertilizer regimes and breeding regions for different genotypes. Maximum benefit can be achieved if the optimum level of fertilizer is applied to the genotypes capable of utilizing these fertilizers.

The study reported here was designed to investigate the following major factors:

1. To study the differential genetic response of control-pollinated progenies of slash pine to applied nitrogen (N), phosphorus (P), and their combination.
2. To determine the magnitude of genotype x fertilizer treatment interaction and other genetic components of variance.
3. To calculate heritability estimates for absorption, translocation, and growth characteristics.
4. To determine genetic correlation between the above factors.
5. To study the movement, and the rate of P incorporation into organic fractions in slash pine seedlings.
6. To determine the relationship between the above P fractions and the growth characteristics.

LITERATURE REVIEW

General

Differential nutrient uptake in agricultural and horticultural crops has been observed for many years. However, evidence of differential responses of forest trees to fertilizers or other environmental factors is rare. Most of the papers related to differential uptake and yield response were reviewed by Vose (1963). He cited the work of Bourcet (1899) who gave one of the earliest reports of differential intraspecific uptake of iodine. Vose also discussed the relationship of nutrient efficiency due to internal and external factors. The internal factors were considered to be associated with a number of physiological processes such as absorption, translocation, assimilation, and other metabolic functions. Differential yield response was separated from differential uptake but they were considered to be closely correlated (Vose, 1963).

Gregory and Crowther (1928) showed that varieties of barley responded differentially to the major nutrient elements. They considered the possibility of developing varieties suitable to deficient soil types.

Smith (1934) studied the differential uptake and yield response of several inbred and hybrid lines of maize to N and P in a culture of sand and solution. He found marked differences in responses among inbred lines to low P, and to a very much lesser extent, to low N. Later, Lyness (1936) conducted an experiment using 21 varieties of maize on several levels of P in sand and solution cultures. A difference in P-absorbing capacity associated with differential yield response was observed. He found that there was more sugar accumulation in the P-inefficient lines than in the P-efficient lines. It was suggested that the differential response of lines to P might be due to the different requirements of lines for P to accelerate respiration for sugar utilization in plant metabolism. He also showed that this P-efficiency was under genetic control. When the P-inefficient line was crossed with P-efficient line the F_1 generation was P-efficient. Therefore, the gene responsible for P-inefficiency appeared to be recessive.

Hoener and DeTurk (1938) studied the growth response of two lines of maize to different levels of N in a solution culture. They noticed that the low-protein plants had greater yield when grown at the lowest level of N, while the high-protein plants had greater yield on solutions with higher N levels. This differential absorption of nitrate was related to a possible "resistance mechanism" to absorption. It was found that the high-protein plants contained more ammonia and amide than the low-protein plants. The authors suggested that this was due to the greater enzymatic capacity for nitrate reduction in the high-protein plants. The low-protein plants, having a lesser capacity for nitrate reduction, formed amide at a rate that could be utilized in protein synthesis. Hence, these plants could not accumulate amide.

Harvey (1939) investigated the absorption and utilization of N in maize and in tomato plants by studying the response of these plants to different levels of N, P, and K in a culture solution. He found a differential response of maize to N source when ammonium and nitrate were used. Harvey reported that the differential responses were due to inherent differences in the genetic constitution of the plants. A significant differential growth response was also observed in the tomato plants.

Hoffer (1926) found differential absorption in six lines of maize growing on clay and loam soils. The ability of selfed lines to absorb K, Fe, and Al was quite different from that of crossed lines. He noticed that the amounts of most minerals in crossed lines were intermediate between those of parents, but K was higher and Fe and Al lower.

The uptake of radioactive P was measured in two inbred lines of maize and their hybrids (Rabideau et al., 1950). A significant differential uptake between inbreds and hybrids was reported.

Gorsline et al. (1961) studied the translocation and accumulation of Ca, Mg, and K in ear-leaves of crosses and in inbred lines of maize and found a differential accumulation of these elements. The differential accumulation was reported to be under genetic control. Similarly, Giosan et al. (1960, cited by Vose, 1963) found varietal differences in absorption of ^{32}P at low temperature among 20 varieties of wheat.

The absorption of K in a number of crops such as oranges, apples, potatoes, soybeans, sugar-beets, and sugar-cane was reviewed by Lawton and Cook (1954). They reported differential absorption of this element in most cases. Later, Rees et al. (1961)

found K, P, and Fe contents of rye genotypes to be quite different.

Large differences in Ca content of white clover were reported by Robinson (1942). He compared the response of various clones and found significant differences among clones, both for percent and total Ca.

The influence of different varieties of rootstocks on the mineral content of the grafted scions constitutes another aspect of genetic control of nutrition. Differential P content was reported for apple trees grafted on different varieties of rootstocks (Vaidja, 1938). A similar result was found for major cations and P in the leaves of apple trees by Wallace (1929). Later, Pearse (1940) demonstrated that the rootstock differentially influenced the response of apple trees to soil nutrients.

The concentration and accumulation of B in the leaves of the scion were investigated by Eaton and Blair (1935). Their experiments were conducted with reciprocally grafted sunflowers, walnuts, lemons, and oranges. They noted that the scion leaf concentrations were higher when grafted onto rootstocks normally accumulating higher B. On the other hand, when grafts were made on the rootstocks of low concentration lines, the accumulation of B in the scion leaf was lower. The fact that the absorption of B was dependent upon the genotype of the rootstocks has raised the question as to whether certain rootstocks can be used more profitably under certain nutritional conditions in orchards.

Differential uptake of Fe and Ca by two maize genotypes was observed by Brown (1967). He reported that the genotype ys_1/ys_1

developed Fe-deficiency on Bladen and Millville soils, whereas the genotype Pa 54 did not show any Fe-deficiency. The Bladen soil was a Cu-deficient soil. When Cu was added to the soil the absorption and translocation of Fe was decreased much more in Pa 54 than in ys_1/ys_1 genotype. In another experiment Brown and Bell (1969) studied absorption and translocation of Fe in ys_1/ys_1 and Pa 54 corn genotypes, grown in nutrient solutions containing different levels of FeHEDTA. They found that Fe stress enhanced the uptake of Fe more in Pa 54 than in ys_1/ys_1 and phosphate reduced Fe uptake more in ys_1/ys_1 than in Pa 54. They concluded that the ys_1/ys_1 genotype had less reducing capacity at the root, requiring less Fe stress for maximum uptake of Fe, and was less tolerant to phosphate. The efficiency of Fe uptake was shown to be controlled by a recessive gene and the causative factor was related to phosphate metabolism. Phosphate appeared to differentially influence metabolic reactions essential to the uptake of Fe in these two genotypes.

Rogers and Thomson (1970) studied N absorption and yield response of a set of diallel progenies of a lolium species (Lolium perenne L.) under different levels of N. They found progeny x nitrogen interaction highly significant for yield and N uptake. Furthermore, the data were analyzed for both general combining ability x nitrogen and specific combining ability x nitrogen interactions. It was found that these interactions were also highly significant. In another experiment by Thomson and Rogers (1970), the utilization and recovery of N in the same plants under 4 levels of N treatment were measured. Only the general combining ability x nitrogen rate interaction was reported to be significant for N utilization.

Forest Trees

During the last two decades estimates of components of genetic and environmental variation for several tree charactersitics have been reported. These include heritability estimates for height growth (Toda et al., 1959; Squillace and Bingham, 1960; Matthews et al., 1960; Squillace and Bengtson, 1961; Hanover and Barnes, 1962; Webb, 1970), for diameter growth (Toda et al., 1959; Matthews et al., 1960; Squillace and Bengtson, 1961), for disease resistance (Bingham et al., 1960), for gum yield (Squillace and Dorman, 1959; Squillace and Bengtson, 1961; Goddard et al., 1962), and for wood quality (Zobel et al., 1962; Stonecypher et al., 1964). However, in most cases the nature and magnitude of interaction components have been overlooked. The inclusion of interactions in heritability estimates will cause an overestimation of genetic gain which should be avoided (Namkoong et al., 1965).

Libby et al. (1969) stated "genotype x environment interaction must be considered with forest trees, as they have not had generations of domestication to eliminate genotypes which are too narrowly adapted." Later, Squillace (1970) discussed the importance of genotype x environment interactions and reviewed most of the papers on this subject. He mentioned that any interaction of genotype x environment is of importance to geneticists and should not be overlooked.

The presence of genotype x environment interactions in several experiments was reported by Wright (1970). He theorized that some of the interactions could be artifacts caused by the persistance of nursery-induced size differences.

Genotype x environment interactions were reported for a number of forest tree species. In a preliminary report on a Monterey pine (Pinus radiata D.) clonal experiment in New Zealand, Burdon (1968) found a significant differential response to environmental conditions. He reported that the greatest clonal differences occurred on a P-deficient site.

Goddard and Vande Linde (1967) found that the one-year-old progenies of slash pine (Pinus elliottii Engelm.) responded differentially in height growth under different sites. However, they reported that the progeny x site interaction had disappeared in the 3-year-old progenies. Later Goddard and Smith (1969) analyzed the height growth of 3-year-old progenies of selected slash pine in 3 different locations (Florida, Alabama, and Georgia) and found a significant line x site interaction.

Kraus (1970) studied genotype x site interactions in 5-year-old progenies of loblolly (Pinus taeda L.) and slash pines. He did not find any significant interaction for height growth or crown width/height ratio in loblolly pine. However, a significant differential response for these traits was reported in slash pine.

Few results on genotype x environment interactions have been reported for hardwoods. Randall and Mohn (1969) grew 79 clones of cottonwood (Populus deltoides Bartr.) on two different sites. The height and diameter growth at 1, 3, and 4 years were measured. A significant clone x site interaction for both traits in all years was reported. Recently, Webb (1970) found a significant family x environment interaction for growth response in American sycamore (Plantanus accidentalis L.).

As forest tree breeders studied genetic variability of different traits, they came to realize the occurrence and significance of genotype x environment interactions in their tests. With some experimental evidence of such interactions available, a new type of interaction became of considerable interest to forest breeders. This was genotype x fertilizer interactions.

Most investigations of genotype x fertilizer interaction in forest tree species were initiated only in recent years. This was associated with interest in forest fertilization which, according to Fowells (1959), appeared to be a profitable practice in specific sites and for some tree species. The significance of fertilizers in forestry and the positive responses of slash pine to fertilizers in Lower Coastal Plain was discussed by Pritchett and Smith (1968) and Pritchett and Llewellyn(1968). Pritchett (1968) reported that superphosphate increased the average volume growth of slash pine on poorly drained soils by 100 percent after 5 to 8 years. The response was reported to vary from 10 percent to 1,600 percent increase.

Among the early workers, Fielding and Brown (1961) detected the differential growth response of Monterey pine to phosphate fertilizers. They discussed the possibility of breeding genotypes capable of growing well on low-quality sites.

Maki (1964), on the basis of observations in a N fertilization study, theorized that certain strains of loblolly pine might respond more favorably to nutrient application than others. He further discussed the possibility of selection and propagation of these strains for breeding programs.

Walker and Hatcher (1965) studied the variation of uptake of nutrients in slash pine progeny groups. They found a significant differential uptake of N and K by seedlings. No differential growth response was reported. In this regard, it was mentioned that the period of study (50 weeks) was not long enough for the seedlings to utilize the absorbed nutrients properly.

Differential response of slash pine to fertilizers has been studied over the past few years at the University of Florida. Goddard and Strickland (1966) and Pritchett and Goddard (1967) investigated the responses of slash pine progenies of selected lines and crosses to irrigation, cultivation, and fertilization. They found a significant differential diameter growth response to fertilization and irrigation in 5-year-old seedlings. Later, Goddard and Strickland (1967) reported the presence of strong genotype x fertilizer interaction in growth of 2-year-old progenies of slash pine.

In a greenhouse study, Goddard and Smith (1969) investigated the response of one-year-old slash pine seedlings to 4 fertilizer treatments. They reported a significant differential height growth response. Recently, Goddard and Strickland (1970) confirmed the presence of strong genotype x fertilizer interaction in open- and control-pollinated progenies of selected slash pine.

Evidence of family x fertilizer interaction in pond pine (Pinus serotina Michx.) was reported by Zobel and Roberds (1970). It was found that the tallest family in the unfertilized plots ranked 4th in the fertilized plots, while the tallest family in the fertilized plots dropped to 11th in the unfertilized plots.

In an experiment with Douglas fir (Pseudotsuga menziesii Mirb.), Rediske et al. (1968) reported a differential dry weight response to fertilizer.

Among hardwoods, the work of Curlin (1967) with cottonwood can be mentioned. He studied the clonal response of cottonwood to N fertilization and found a significant clone x fertilizer interaction for height, diameter, and volume growth. Curlin pointed out that it is profitable to select eastern cottonwood under a nutritional environment comparable to that ultimately to be used in production plantings.

It should be noted, however, that genotype x fertilizer interaction is not limited to uptake, accumulation of nutrients in plant organs, or growth characteristics. Genotype x fertilizer and genotype x environment interactions have been reported for other traits such as wood quality, seed production, survival and crown size. The work of Bergman (1968), Bengtson and Goddard (1966) for cone crop; Borsdorf (1965), Posey (1965) for wood characteristics; Stonecypher (1966) for survival; and Squillace and Fisher (1966) for turpentine composition can be mentioned. Most of the published and unpublished papers on genotype x fertilizer interaction were reviewed by Zobel and Roberds (1970), who pointed out that genotype x fertilizer interaction must be taken into account if forestry is to achieve its potential.

CONTROL-POLLINATED EXPERIMENT

Plant Materials

Seeds used in this experiment were from control-pollinated select slash pine trees in the University of Florida's seed orchard. Pollen from 5 male parents were used to pollinate 5 female parents. The cones were collected in 1968. Some of the crosses did not produce enough seeds for inclusion in the experiment. Therefore, all 25 possible combinations were not used (see experimental design).

The male parents were identified as 1-60, 5-62, 12-57, 98-56, and 196-58. The female parents were 17-57, 87-56, 254-55, 262-55, and 268-55 (the last two digits only refer to the year the parents were selected and therefore will not be repeated hereafter).

The seedlings were grown from seeds planted April, 1968, in the local nursery. After a period of 8 months, the seedlings were potted and transferred into the greenhouse.

Greenhouse Procedure

Soil and Potting

The soil was collected from an area north of Port St. Joe, in Gulf County, Florida. The soil type was a Bladen loamy fine sand, which is especially low in extractable P (Table 1). The soil was ground and mixed thoroughly. It was passed through a screen for textural uniformity and separation of any undesirable debris.

Table 1. Chemical characteristics of Bladen loamy fine sand used in the experiment[a]

K	Ca	Mg	P	N		pH	CEC
				Exchangeable	Total		
ppm							meq/100g
11	45	48	0.28	50	720	4.9	4.135

[a] K, Ca, Mg, and P are NH_4OAc (pH 4.8) extractable. Exchangeable N was in form of NH_4^+, extracted with N KCl solution. pH was determined in water solution and CEC by NH_4OAc (pH 7.0) replacement.

Soil analyses for K, Ca, Mg, and P were carried out by the Department of Soil Science, University of Florida, according to their standard procedure. Exchangable N was determined by saturation of soil samples in N KCl and determining the N in extract. Total N was determined by the micro-Kjeldahl method, using 2.0 g of soil sample. The pH values were determined by measurement of the acidity of the water solution of soil samples with a pH meter. Cation exchange capacity (CEC) was measured by NH_4^+ (pH 7.0) replacement.

Deep plastic containers (28 x 26 x 15 cm in depth, length, and width, respectively), with no drainage system, were used. Each container was filled with 9.5 kg of oven-dry soil.

Seedlings, uniform in size (within each full-sib family) were planted in pots on January 7, 1969. The roots of the seedlings were washed with tap water just prior to potting.

The initial height and basal diameter were measured one week after potting, to the nearest cm and mm, respectively.

Fertilizer Treatments

The soil was treated with N and P one month after potting. This period was allowed for seedling establishment before the fertilizer application. Nitrogen was in the form of urea (NH_2CONH_2), at a rate of 100 ppm. Phosphorus was in the form of monocalcium phosphate ($CaH_4(PO_4)_2 \cdot H_2O$), at a rate of 50 ppm. Both additions were on the basis of soil oven-dry weight.

Four different combinations of N and P were used. They were (in ppm) as follows:

N_0P_0, $N_{100}P_0$, $N_{100}\ P_{50}$, and N_0P_{50}

Total treatments were applied in 6 equal increments during a 3-week period. The range of N and P contents between the native and fertilized soils provided a suitable substrate for detection of genotype x fertilizer treatment interaction.

The seedlings were regularly watered with de-ionized water throughout the period of experiment.

Experimental Design

A balanced incomplete randomized block design with 3 replications was used. This design was selected because of insufficient seeds in some of the crosses. Out of 25 possible combinations of factorial mating design (5 female x 5 male), only 20 crosses (families) were used.

Each cross was represented by 4 full-sibs in each replication, which totaled 12 in the experiment. Fertilizer treatments were randomly assigned to each of the 4 full-sibs in the replication. The allocation of seedlings to the replications was also random. A total of 240 seedlings was used in the experiment (Fig. 1).

Final Measurements

The seedlings were harvested on May 30, 1970 (25 months after germination or 16 months after fertilizer treatment). This allowed one full growing season and the first flush of the second season. The height, basal diameter, and fresh weight of top (stem, branches, and needles) were measured. Soil samples were taken for analysis, and the roots were washed out of the pots.

REPLICATION I

		MALE PARENTS				
		1	5	12	98	196
FEMALE PARENTS	17	N P NP Control				†
	268				†	
	254			†		
	262		†			
	87	†				

REPLICATION II
(same as replication I)

REPLICATION III
(same as replication I)

†Missing crosses

Fig. 1. Control-pollinated experimental design.

The roots and the top were dried to constant weight in a temperature room (70 C) for a period of 2 weeks. The needles were stripped and the dry weights of the roots, stem and branches, and needles of each seedling were determined.

Laboratory Procedures

Sample Preparation

The plant material was first ground in a large Wiley mill. The roots, the stem and branches, and the needles were ground separately for each seedling. For each part, the tissue was mixed well and a subsample was taken. The subsample was then ground in an intermediate Wiley mill to pass a 20-mesh screen. The ground tissues were stored in closed containers for later analyses.

Nitrogen Determination

The percent and total accumulated N were determined for roots, stem and branches, and needles. Total N was determined by the micro-Kjeldahl method (Bradstreet, 1965), with modifications of catalyst and indicator. The catalyst was commercial "Kel pak" and the indicator was commercial "N-point". Ammonium generated was determined by titration, expressed as N percent of weight, and combined with tissue weights for calculating total N accumulation.

Phosphorus Determination

The percent and total accumulated P in roots, stem and branches, and needles were measured for each seedling. Total P was determined by the Elon method (Cavell, 1955). One g of tissue was ashed in a furnace and aliquots of digested and diluted samples prepared. One ml of this aliquot was used for spectrophotometric test. The absorbance was read in a Beckman DB spectrophotometer at a wavelength of 650 μ. A standard curve was constructed and the absorbance values were converted to ppm. These values were then converted to percent of sample and combined with tissue weights for determining the total P accumulation in each sample.

Statistical Analyses

Linear Model

For proper evaluation of experimental data, a model had to be specified. It was assumed that the treatment effect was fixed and that the male and female effects were random. Accordingly, a mixed model was used (Steel and Torrie, 1960).

The linear model for the experiment was considered as follows:

$$X_{hijkl} = \bar{\mu} + f_j + m_k + r_h + t_l + (fm)_{jk} + (ft)_{jl} + (mt)_{kl} + (fmt)_{jkl} + e_{hijkl}$$

where:

X_{hijkl} = observation on the i^{th} individual progeny of the j^{th} female and the k^{th} male in the h^{th} replication affected by the l^{th} fertilizer treatment

$\bar{\mu}$ = population mean

f_j = effect of j^{th} female parent

m_k = effect of k^{th} male parent

r_h = effect of h^{th} replication

t_l = effect of l^{th} fertilizer treatment

$(fm)_{jk}$, $(ft)_{jl}$, $(mt)_{kl}$, and $(fmt)_{jkl}$ = interaction effects

e_{hijkl} = error term, including higher order interactions.

Expected Mean Squares

The components of the expected mean squares for different factors are given in Table 2. The coefficients were adjusted for the missing crosses and the fixed effect of fertilizer treatments (Steel and Torrie, 1960).

Adjustment for Missing Crosses

The sums of squares (SS) for the female, male, female x fertilizer treatment, and male x fertilizer treatment were adjusted for incomplete blocks. The adjustment was made according to Cochran and Cox (1950). The adjusted sum of squares for the female were calculated by the following formula:

$$\text{Adjusted female SS} = \frac{(m-1) \sum Q^2}{t[trmk(k-1)]}$$

where:

$Q = kF - M$

F = total values for all crosses, having a common female parent

M = total values for all crosses, having a common male parent

The adjusted male sum of squares was calculated as follows:

Adjusted male SS = adjusted female SS + unadjusted male SS − unadjusted female SS.

The adjusted female x fertilizer treatment sum of squares was calculated on the same basis as for the adjusted female sum

Table 2. General form of analysis of variance and the components of expected mean squares

Source of Variation	Degrees of Freedom[†]	Expected Mean Squares[††]
Replications	r-1	$\sigma_e^2 + tc\,\sigma_R^2$
Treatments[†††](T)	t-1	$\sigma_e^2 + r\frac{t}{t-1}\sigma_{CxT}^2 + rc\,\sigma_T^2$
Crosses (C)	c-1	$\sigma_e^2 + rt\,\sigma_C^2$
Female (F)	f-1	$\sigma_e^2 + rt\,\sigma_{FxM}^2 + rtk'\,\sigma_F^2$
Male (M)	m-1	$\sigma_e^2 + rt\,\sigma_{FxM}^2 + rtk\,\sigma_M^2$
FxM	(c-1)-(f+m-2)	$\sigma_e^2 + rt\,\sigma_{FxM}^2$
CxT	(c-1)(t-1)	$\sigma_e^2 + r\frac{t}{t-1}\sigma_{CxT}^2$
FxT	(f-1)(t-1)	$\sigma_e^2 + r\frac{t}{t-1}\sigma_{FxMxT}^2 + rk'\frac{t}{t-1}\sigma_{FxT}^2$
MxT	(m-1)(t-1)	$\sigma_e^2 + r\frac{t}{t-1}\sigma_{FxMxT}^2 + rk\frac{t}{t-1}\sigma_{MxT}^2$
FxMxT	(t-1)(c-f-m+1)	$\sigma_e^2 + r\frac{t}{t-1}\sigma_{FxMxT}^2$
Residual	n-(r+ct-1)	σ_e^2
Total	n-1	

[†] Degrees of freedom were determined with consideration of missing crosses.

r = number of replications

t = number of fertilizer treatments

Table 2. (continued)

c = number of crosses

f = number of female parents

m = number of male parents

n = total number of seedlings in the experiment

†† Components are defined as follows:

σ^2_e = error variance

σ^2_R = replication variance

σ^2_C = variance due to differences among crosses

σ^2_T = variance due to differences among fertilizer treatments

σ^2_{CxT} = variance due to differences among cross x fertilizer treatments interaction

σ^2_F = variance due to differences among female parents

σ^2_M = variance due to differences among male parents

σ^2_{FxM} = variance due to female x male interactions (variance among specific combining ability of parents)

σ^2_{FxT} = variance due to female x fertilizer treatments interactions

σ^2_{MxT} = variance due to male x fertilizer treatments interactions.

σ^2_{FxMxT} = variance due to female x male x fertilizer treatments interactions (variance due to specific combining ability x fertilizer treatments interactions)

k = number of male parents mated to each female parent

k' = number of female parents mated with each male parent

††† Treatments will indicate fertilizer treatments in all tables.

of squares. The following formula was used:

$$\text{Adjusted female x fertilizer treatment SS} = \frac{(m-1)\sum Q'^2}{trmk(k-1)}$$

$$- \text{ adjusted female SS.}$$

where:

$Q' = kF' - M'$

F' = total values for all crosses, having a common female parent and treated with the same fertilizer

M' = total values for all crosses, having a common male parent and treated with the same fertilizer

Adjusted male x fertilizer treatment sum of squares was calculated as follows:

Adjusted male x fertilizer treatment SS =

adjusted female x fertilizer treatment SS
+ unadjusted male x fertilizer treatment SS
- unadjusted female x tertilizer treatment SS.

Heritability

Heritability (h^2) estimates were determined for general and local adaptability according to Dickerson (1961). Heritability formulae for general adaptability, used in this study, were as follows:

$$h_F^2 = \frac{4\sigma_F^2}{\sigma_F^2 + \sigma_M^2 + \sigma_{FxM}^2 + \sigma_{FxT}^2 + \sigma_{MxT}^2 + \sigma_{FxMxT}^2 + \sigma_e^2/r}$$

$$h_M^2 = \frac{4\sigma_M^2}{\sigma_F^2 + \sigma_M^2 + \sigma_{FxM}^2 + \sigma_{FxT}^2 + \sigma_{MxT}^2 + \sigma_{FxMxT}^2 + \sigma_e^2/r}$$

$$h_{F+M}^2 = \frac{2(\sigma_F^2 + \sigma_M^2)}{\sigma_F^2 + \sigma_M^2 + \sigma_{FxM}^2 + \sigma_{FxT}^2 + \sigma_{MxT}^2 + \sigma_{FxMxT}^2 + \sigma_e^2/r}$$

where:

h_F^2 = heritability estimate for female parent under general adaptability

h_M^2 = heritability estimate for male parent under general adaptability

h_{F+M}^2 = combined heritability estimate for female and male parents under general adaptability

It is considered that female or male component of variance for half-sib families estimates one-quarter of the additive genetic variance. Theoretically, both heritability estimates (h_F^2 for female parent and h_M^2 for male parent) are equally reliable, and their combination (h_{F+M}^2) may be taken as the best estimate (Falconer, 1960).

For local adaptability the following heritability formulae were used:

$$h_F^2 = \frac{4\sigma_F^2 + \sigma_{GxT}^2}{\sigma_F^2 + \sigma_M^2 + \sigma_{FxM}^2 + \sigma_{FxT}^2 + \sigma_{MxT}^2 + \sigma_{FxMxT}^2 + \sigma_e^2/r}$$

$$h_M^2 = \frac{4\sigma_M^2 + \sigma_{GxT}^2}{\sigma_F^2 + \sigma_M^2 + \sigma_{FxM}^2 + \sigma_{FxT}^2 + \sigma_{MxT}^2 + \sigma_{FxMxT}^2 + \sigma_e^2/r}$$

$$h_{F+M}^2 = \frac{2(\sigma_F^2 + \sigma_M^2) + \sigma_{GxT}^2}{\sigma_F^2 + \sigma_M^2 + \sigma_{FxM}^2 + \sigma_{FxT}^2 + \sigma_{MxT}^2 + \sigma_{FxMxT}^2 + \sigma_e^2/r}$$

where:

h_F^2 = heritability estimate for female parent under local adaptability

h_M^2 = heritability estimate for male parent under local adaptability

h_{F+M}^2 = combined heritability estimate for female and male parents under local adaptability

σ_{GxT}^2 = genotype x fertilizer treatment interaction, defined as

$\sigma_{GxT}^2 = \sigma_{FxT}^2 + \sigma_{MxT}^2 + \sigma_{FxMxT}^2$

General adaptability is a case in which the performance of the future generations are not considered to be under the same environmental conditions as those under the experimental conditions, while local adaptability is the case under which the control of the future mean of environmental factors is possible (Dickerson, 1961).

Phenotypic Variance

The components of phenotypic variance, adapted from Dickerson (1961) and Hanson (1961), were as follows:

$$\sigma_P^2 = \sigma_F^2 + \sigma_M^2 + \sigma_{FxM}^2 + \sigma_{FxT}^2 + \sigma_{MxT}^2 + \sigma_{FxMxT}^2 + \sigma_e^2/r$$

The above components of variance were determined using the expected mean squares in Table 2.

Genetic Correlation

In order to calculate the genetic correlation between two traits, the estimates of genetic components of covariance for the given traits should be determined. According to Falconer (1960), the components of covariance can be determined from analysis of covariance, having expectation values for the cross products similar to those of expected mean squares in analysis of variance. In this experiment, the components of covariance for female and male parents were determined by covariance analysis similar to Table 2.

The components of covariance have the same genetic interpretation as the components of variance (Falconer, 1960). Thus, the component of covariance for male or female parents estimates one-quarter of the additive genetic covariance of two traits. Similarly, the average value of components of female and male covariance can be considered as one-quarter of the covariance of the additive values of two traits.

The following formula was used for estimation of genetic correlation:

$$r_A = \frac{\mathrm{Cov}_{A_{XY}}}{\sqrt{\sigma^2_{A_X} \cdot \sigma^2_{A_Y}}}$$

where:

r_A = genetic correlation between traits X and Y (i.e., the correlation of breeding values).

$$\mathrm{Cov}_{A_{XY}} = 4\left(\frac{\mathrm{Cov}_{F_{XY}} + \mathrm{Cov}_{M_{XY}}}{2}\right) = \text{additive genetic covariance of traits X and Y}$$

$$\sigma^2_{A_X} = 4\left(\frac{\sigma^2_{F_X} + \sigma^2_{M_X}}{2}\right) = \text{additive genetic variance of trait X}$$

$$\sigma^2_{A_Y} = 4\left(\frac{\sigma^2_{F_Y} + \sigma^2_{M_Y}}{2}\right) = \text{additive genetic variance of trait Y}$$

$\mathrm{Cov}_{F_{XY}}$ and $\mathrm{Cov}_{M_{XY}}$ are components of covariance of traits X and Y for female and male, respectively.

$\sigma^2_{F_X}$ and $\sigma^2_{M_X}$ are components of variance of trait X for female and male, respectively.

$\sigma^2_{F_Y}$ and $\sigma^2_{M_Y}$ are components of variance of trait Y for female and male, respectively.

EXPERIMENT WITH ^{33}P

Materials and Methods

Sand Culture

Open-pollinated seeds of 3 female parents, used in the control-pollinated experiment, were germinated in Petri dishes. The germinated seeds were transferred into small polyvinyl chloride tubes (15 cm in length and 3 cm in diameter) filled with acid-washed sand. The tubes were placed uniformly and randomly in pots. The spaces between the tubes were also filled with acid-washed sand. The pots were fed from the bottom by a tube connected to a nutrient reservoir solution which was placed at a higher elevation.

There were 3 seedlings of each line in each pot. A total of 5 pots, each connected to a different nutrient solution, was used. Seedlings were grown for a period of 4 months before treatment with ^{33}P.

Nutrient Solutions

Each pot was treated with a mixture of 2 different nutrient solutions. The basic solution was a modified Shive and Robbins solution (1942). This solution was made one-tenth strength with no N and P. The solution supplied each pot was supplemented with one of five different combinations of N and P. These combinations (in ppm) were as follows:

$N_{100}P_{50}$, $N_{50}P_{50}$, $N_{10}P_{1}$, $N_{50}P_{5}$, and $N_{50}P_{100}$

Nitrogen was in the form of urea and P in the form of phosphoric acid. The pots were adjusted so that they held the same volume of nutrient solution.

The solutions were applied 3 times per week from the bottom and drained one hour after the pots were filled. By this arrangement all seedlings within each pot were supplied with the same kind and volume of nutrient solution and for the same period of time, and the seedlings in different pots with the different nutrient solutions also received the same volume for the same period of time.

Treatment with ^{33}P

A total of 9 seedlings from each pot (3 seedlings in each of 3 lines) were washed out of the tubes. Attention was given to preventing any damage to the root system during the washing. The roots were cleaned and rinsed with distilled water. For each treatment, 9 seedlings were mounted on the top of a pot containing the labeled nutrient solution. The root system of each seedling was uniformly immersed in nutrient solution down to the root collar. Each group of 9 seedlings was exposed to the same nutrient treatment given during the sand culture period. The pH of the labeled solutions was adjusted to 5.0.

Phosphorus--33 was added to each pot containing 500 ml of solution at initial activity of 100 µci/500 ml. Air was bubbled into each solution for one hour prior to seedling immersion to provide sufficient oxygen for the roots.

The pots containing the seedlings were placed in a growth chamber for a period of 15 hours. The seedlings were subjected to relative humidity of 80 percent and temperature of 70 C with continuous light.

Phosphate Fractionation

Seedlings were taken out of the labeled solutions and the roots passed through 5 series of distilled water to remove ^{33}P from the free spaces. Arrangements were made so that all seedlings were exposed to ^{33}P for the same period and remained for equal times in distilled water rinses.

The roots were separated from the shoots at root collar. Height and fresh weight were determined. The roots and shoots were then frozen in liquid nitrogen and placed in a freezer.

The phosphate fractionation was carried out by the modified method of Ogur and Rosen (1950), used by Loughman and Russell (1957). A further modification for the acid-soluble fraction was also applied (Rovira and Bowen, 1966; Bowen, 1969).

The tissue was crushed in mortar containing liquid nitrogen and homogenized in 5 ml of 0.1 $\underline{N}$ $HClO_4$. The acid-soluble fraction was separated by 5 series of freezings (at - 70 C) and thawings in 5 ml of 0.1 $\underline{N}$ $HClO_4$. This procedure was followed by washing the tissue with distilled water at 1 - 2 C 3 times (Bowen, 1969).

The DNA and RNA fractions were removed according to procedures described by Loughman and Russell (1957). The clear separation of these two fractions was considered doubtful by Hutchison and Munro (1961), and Bowen (1969). Therefore, the data for these two fractions were pooled.

The phospholipid-phosphoprotein fraction was removed by 2 N NaOH and 2 N HCl (Ogur and Rosen, 1950). The fractionation procedure is given in Fig. 2.

Radioactivity Measurement

Each fraction was evaporated to dryness in a liquid scintillation vial under low temperature. The activity of an aliquot of sample was measured in a liquid scintillation spectrometer. Activity was corrected for color quench, using a standard curve. The standard curve was constructed using samples of known activities added to nonradioactive sample aliquots yielding colors in the range of the experimental samples.

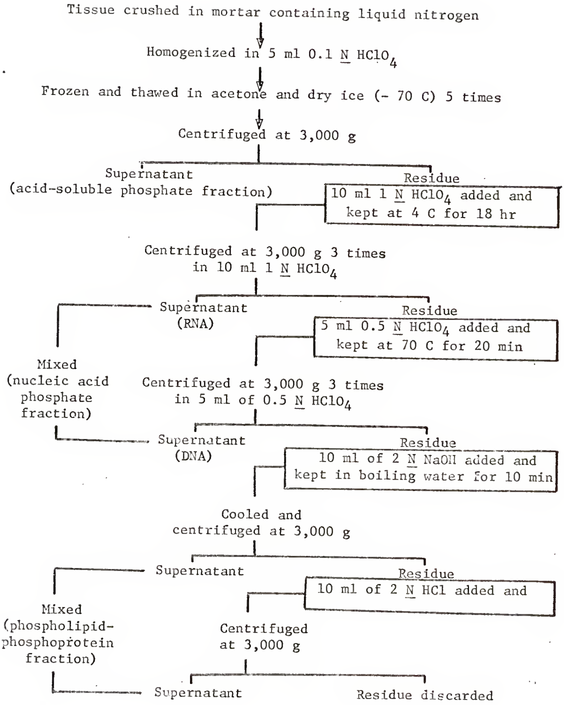
Tissue crushed in mortar containing liquid nitrogen
Homogenized in 5 ml 0.1 N $HClO_4$
Frozen and thawed in acetone and dry ice (- 70 C) 5 times
Centrifuged at 3,000 g
Supernatant (acid-soluble phosphate fraction)
Residue
10 ml 1 N $HClO_4$ added and kept at 4 C for 18 hr
Centrifuged at 3,000 g 3 times in 10 ml 1 N $HClO_4$
Supernatant (RNA)
Residue
5 ml 0.5 N $HClO_4$ added and kept at 70 C for 20 min
Mixed (nucleic acid phosphate fraction)
Centrifuged at 3,000 g 3 times in 5 ml of 0.5 N $HClO_4$
Supernatant (DNA)
Residue
10 ml of 2 N NaOH added and kept in boiling water for 10 min
Cooled and centrifuged at 3,000 g
Supernatant
Residue
10 ml of 2 N HCl added and
Mixed (phospholipid-phosphoprotein fraction)
Centrifuged at 3,000 g
Supernatant
Residue discarded

Fig. 2. Steps in phosphate fractionation for ^{33}P experiment.

RESULTS AND DISCUSSION
OF CONTROL-POLLINATED EXPERIMENT

Soil Nutrient Content

Variation in soil nutrient content and soil acidity can cause variation in slash pine growth. When variation in growth is observed among trees receiving the same fertilizer treatment, it is necessary to establish that there is no significant variation in soil factors before presumption of genetic variation. To determine uniformity of soil factors, three samples were analyzed for each of the fertilizer treatments. There were no significant differences in the nutrients or in the acidity of similarly treated soils. There were, however, large differences in N and P content and a small difference in the acidity of soils under the different fertilizer treatments (Table 3). Therefore, the differences in growth response of the crosses, under the same fertilizer treatment, were not related to soil variation.

Growth Characteristics

Height and Diameter Growth and Fresh Weight

Height and diameter growth data, representing growth after application of fertilizers, were analyzed according to the statistical procedures outlined previously. Results of analyses of variance indicated these traits were significantly different among the crosses (Table 4). Most of the variation was due to female x male interaction. The effects of female and male parents were

Table 3. Nutrient content and acidity of soil at end of experiment[a]

Treatments	Soil Samples	K	Ca	Mg	P	N		pH
						Exchangeable	Total	
		ppm						
$N_{100}P_0$	1	11	40	42	0.43	42	793	4.9
	2	12	36	38	0.35	48	785	4.8
	3	12	39	45	0.40	43	776	4.9
N_0P_{50}	1	10	75	48	3.57	22	661	4.9
	2	12	72	40	3.95	30	680	5.0
	3	14	60	37	3.82	25	698	4.9
$N_{100}P_{50}$	1	15	105	56	3.66	41	766	5.1
	2	15	90	50	3.90	40	782	5.1
	3	18	93	59	3.86	46	785	5.2
Control	1	10	45	42	0.28	22	705	4.9
	2	10	45	48	0.33	27	718	4.9
	3	12	44	48	0.25	30	732	4.8

[a] K, Ca, Mg, and P are NH_4OAc (pH 4.8) extractable. Exchangeable N was in the form of NH_4^+, extracted with N KCl solution, and pH was determined in water solution.

Table 4. Summary of analyses of variance for height growth, diameter growth, and fresh weight of top

Source of Variation	Degrees of Freedom	Mean Squares		
		Height Growth	Diameter Growth	Top Fresh Weight
Replications	2	101.9042	0.0335	286.9042
Treatments (T)	3	6,561.6944***	3.8959***	614,330.5611***
Crosses (C)	19	453.6427***	0.0610***	8,784.4131***
Female (F)	4	698.9826	0.0430	17,349.0881
Male (M)	4	614.5555	0.1279^{+}	4,904.8069
FxM	11	305.9145***	0.0424*	7,080.7517***
CxT	57	208.7917***	0.0332***	2,791.3739**
FxT	12	169.4298	0.0284	4,450.1983^{+}
MxT	12	296.2250	0.0418	2,600.9588
FxMxT	33	191.1558***	0.0319*	2,257.4069*
Residual	158	53.3037	0.0205	1,606.2375
Total	239			

$^{+}$Significant at 0.10 level.

*Significant at 0.05 level.

**Significant at 0.01 level.

***Significant at 0.005 level.

not significant for height growth and fresh weight of top. However, the differences in male parents for diameter growth were found to be significant at the 10 percent level (Table 4).

The presence of highly significant female x male interaction (mostly due to nonadditive genetic factors) suggests the utilization of specific combining ability rather than general combining ability in future programs. For example, when female parent 87 was pollinated with pollen from male parent 98, the progenies grew well under the N and P deficient (control) soil. However, when the same female parent was pollinated with a different male parent (male 196), the progenies were much shorter than their maternal half-sibs under the same treatment (Fig. 3).

Genotype x fertilizer treatment interactions for the above traits were highly significant. The differences were mostly due to the interaction of female x male x fertilizer treatment (Table 4). Differential growth response to fertilizers can clearly be seen in height growth. Some of the crosses grew well under one fertilizer treatment but poorly under other fertilizer treatments. The parents effectively changed the response of their progenies to fertilizers (Fig. 4). In the upper photograph of Fig. 4, cross 262 x 196 had the best height growth under NP treatment, while in the lower photograph cross 262 x 1-60 had the best growth under P treatment and lowest under NP treatment.

The female parents also affected the response of their progenies to fertilizers (Fig. 5). In the upper photograph cross 87 x 98 had third rank in height growth under NP treatment,

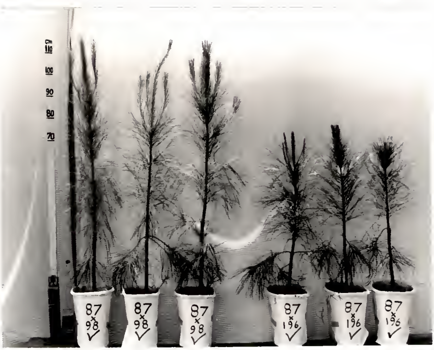

Fig. 3. The effects of male parents in changing the height growth of their progenies under the same treatment.

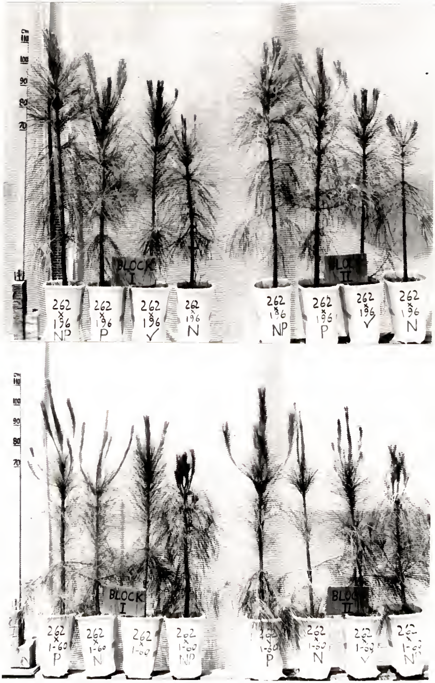

Fig. 4. The effects of male parents in changing the height growth of their progenies to fertilizer treatments differentially.

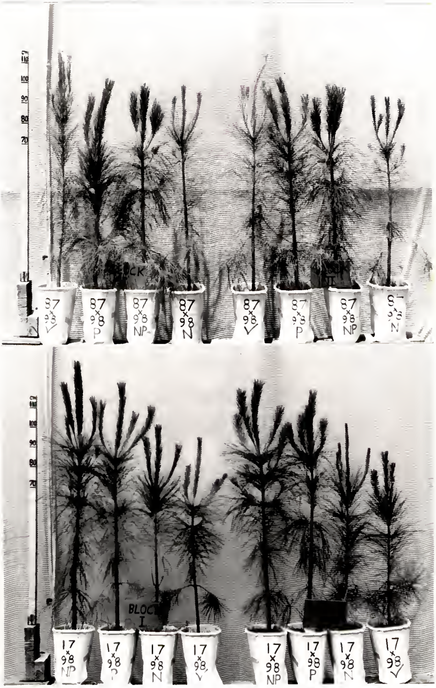

Fig. 5. The effects of female parents in changing the height growth of their progenies to fertilizer treatments differentially.

while in the lower photograph cross 17 x 98 was tallest under the NP treatment.

The strong genotype x fertilizer treatment interaction suggests the need for considering specific combining ability when breeding for different fertilizer regimes.

The effect of fertilizer treatments (per se) on the growth response of crosses was higher than other factors. On the average, and regardless of genotype x fertilizer treatment interaction, seedlings grew taller with added P. However, the highest diameter growth and top fresh weight were obtained in seedlings treated with NP (Table 5). The top fresh weight was affected more by diameter growth than height growth.

Data for mean values of crosses and general combining ability of parents for the above traits (regardless of fertilizer effects) are shown in Table 6. Among female parents, the greatest value for general combining ability belonged to tree 17 and the lowest to tree 268. Ranking of general combining ability of female parents for diameter growth and fresh weight of top was not the same as that of height growth. The parents which produced the tallest seedlings failed to produce the progenies with maximum diameter growth (Table 6). For example, female 254, which was intermediate in height growth and second in diameter growth, produced the maximum amount of fresh weight. On the other hand, female 268, which produced the shortest progenies and ranked third in diameter growth, produced the least amount of wood and foliage. A similar pattern was noted for the general combining ability of male parents (Table 6).

Table 5. Mean values of seedlings under different fertilizer treatments[a]

Characteristics	Control	N	P	NP
Height Growth after Fertilization[b] (cm)	64.75	56.13	79.73	74.27
Diameter Growth after Fertilization[b] (cm)	0.93	0.94	1.29	1.44
Top Fresh Weight[b] (g)	245.97	224.07	365.55	438.18
Dry Weight of Roots[c] (g)	32.35	33.60	43.41	60.73
Dry Weight of Stem and Branches[c] (g)	48.89	42.62	67.32	70.62
Dry Weight of Needles[c] (g)	34.34	25.66	54.14	70.20
Top Dry Weight[d] (g)	83.23	68.28	121.46	140.82
Total Dry Weight of Seedlings[d] (g)	115.58	101.88	164.87	201.55

[a] Values are the average of 60 seedlings (3 replications of 20 crosses) in each of the fertilizer treatments.

[b] Differences among means of height growth, diameter growth, and top fresh weight greater than 2.85. 0.06, and 15.63, respectively, are significant at 0.05 level, and greater than 3.68, 0.07, and 20.18 are significant at 0.01 level.

[c] Differences among means of dry weight of roots, stem and branches and needles greater than 2.40, 2.70, and 2.87, respectively, are significant at 0.05 level, and greater than 3.10, 3.49, and 3.70 are significant at 0.01 level.

[d] Differences among means of top and total dry weight greater than 4.98 and 6.23, respectively, are significant at 0.05 level, and greater than 6.40 and 8.04 are significant at .01 level.

Table 6. Mean of height[a] (Ht), diameter[a] (Dia), and top fresh weight (F Wt) of the crosses[b] and general combining ability of the parents[c]

			MALE PARENTS					
		1	5	12	98	196	Mean	(Rank)
FEMALE PARENTS 17	Ht (cm)	73.58	72.66	71.00	79.00		74.06	(1)
	Dia (mm)	1.13	1.09	1.14	1.13		1.12	(4)
	F Wt (g)	325.7	325.3	304.1	332.9		322.00	(2)
268	Ht (cm)	62.58	62.58	58.00		63.33	62.29	(5)
	Dia (mm)	1.12	1.02	1.28		1.13	1.14	(3)
	F Wt (g)	264.1	271.7	322.7		302.0	290.13	(5)
254	Ht (cm)	68.33	67.33		79.50	66.00	70.29	(3)
	Dia (mm)	1.19	1.09		1.15	1.20	1.16	(2)
	F Wt (g)	362.0	323.9		376.8	337.5	350.05	(1)
262	Ht (cm)	71.08		66.75	63.66	62.00	65.87	(4)
	Dia (mm)	1.17		1.28	1.15	1.19	1.20	(1)
	F Wt (g)	333.1		290.2	325.7	324.5	318.38	(3)
87	Ht (cm)		72.00	69.58	79.83	62.91	71.08	(2)
	Dia (mm)		0.99	1.08	1.18	1.16	1.10	(5)
	F Wt (g)		391.1	304.9	332.1	290.0	311.53	(4)
Mean and (Rank)	Ht (cm)	69.56 (2)	68.64 (3)	66.33 (4)	75.50 (1)	63.56 (5)	Pop mean	68.72
	Dia (mm)	1.15 (3,4)	1.05 (5)	1.20 (1)	1.15 (3,4)	1.17 (2)	Pop mean	1.14
	F Wt (g)	321.23 (2)	310.00 (4)	305.48 (5)	341.88 (1)	313.50 (3)	Pop mean	318.4

[a] The values for height and diameter are growth after fertilization.

[b] Differences among means of crosses for height, diameter, and top fresh weight greater than 7.31, 0.14, and 40.14, respectively, are significant at 0.05 level, and greater than 9.29, 0.18, and 51.02 are significant at 0.01 level.

[c] Differences among means of male parents for diameter growth greater than 0.09 are significant at 0.05 level.

Dry Weights of Plant Portions

Dry weights of roots, stem and branches, and needles were determined separately. Analysis of variance showed highly significant differences among crosses for the above traits. Except for the effect of female parents on dry weight of needles, differences among the other traits were not due to a significant effect of male or female parents (Table 7).

Most of the differences among the crosses were associated with female x male interaction (Table 7). This was also true for height and diameter growth and fresh weight of top.

In the case of roots, the additive genetic effect was not present at all. No or very low additive genetic effect in root growth of pine was previously reported by Bilan (1960) and Stonecypher et al. (1966). In this study, root growth was highly affected by fertilizer treatments. The diversity of soil nutrient completely masked the possible low additive genetic variation in root growth. This was expected from theory because the expansion of population of environments will increase the genotype x environment interaction variance at the expense of additive variance. A high effect of genotype x fertilizer treatment interaction was observed in root growth (Table 7).

The dry weights of stem and branches and needles showed also a highly significant differential response. This differential response was mostly due to the female x male x fertilizer treatment interaction and to a lesser degree due to the female x fertilizer treatment and male x fertilizer treatment interactions (Table 7).

Table 7. Summary of analyses of variance for dry weight of roots, stem and branches, and needles

Source of Variation	Degrees of Freedom	Mean Squares		
		Roots Dry Weight	Stem and Branches Dry Weight	Needles Dry Weight
Replications	2	392.7875^{***}	57.7792	55.8842
Treatments (T)	3	$10,310.4944^{***}$	$11,296.1597^{***}$	$24,155.1042^{***}$
Crosses (C)	19	243.6587^{***}	382.6842^{***}	420.0568^{***}
Female (F)	4	256.8756	663.9527	837.5777^{+}
Male (M)	4	165.6360	344.3173	247.5673
FxM	11	266.4972^{***}	294.3786^{***}	330.9544^{***}
CxT	57	91.9447^{***}	161.9462^{***}	143.6509^{***}
FxT	12	138.1488^{*}	284.4981^{*}	260.7587^{**}
MxT	12	123.9926^{+}	118.6821	178.5122^{*}
FxMxT	33	63.4894^{*}	133.1143^{***}	88.3894^{*}
Residual	158	37.8128	48.0112	54.1407
Total	239			

$^{+}$Significant at 0.10 level.

*Significant at 0.05 level.

**Significant at 0.01 level.

***Significant at 0.005 level.

Mean values for the crosses and general combining ability of parents for these traits are given in Table 8. Except in a few cases, the ranking of general combining ability of parents was not the same for these traits. The parents which produced progenies with greater root growth did not necessarily produce progenies with more wood or needles (Table 8).

Fertilizer treatments had pronounced effects on the growth of roots, stem and branches, and needles. Regardless of genotype x fertilizer treatment effect, the highest values for the above traits were obtained in NP-treated seedlings (Table 5). However, the lowest values were not found in the same treatment for all traits. For example, lowest needle dry weight was obtained in seedlings treated with N, while the lowest value for the dry weight of roots belonged to seedlings grown with no fertilizer (control).

Top and Total Dry Weight

The nature of variation for top and total dry weights was found to be similar (Table 9). These traits also showed similar results to those of dry weight of stem and branches and needles, when subjected to analyses of variance.

The main factor influencing the variability among crosses was female x male interaction. While no significant variation among males for these traits was observed, the effect of female parents was high (Table 9). Lack of significant variation among male parents for these traits was considered to be due to the lack of additive variability among the needles for male parents. This is discussed further

Table 8. Mean dry weight of roots (R Wt), stem and branches (S Wt), and needles (N Wt) of the crosses[a] and general combining ability of the parents[b]

		MALE PARENTS						
FEMALE PARENTS		1	5	12	98	196	Mean	(Rank)
17	R Wt (g)	40.58	46.75	32.24	38.83		39.61	(5)
	S Wt (g)	57.17	55.75	55.42	59.92		57.07	(3)
	N Wt (g)	48.58	48.33	41.42	47.42		46.44	(2)
268	R Wt (g)	39.50	40.89	44.42		44.83	42.41	(2)
	S Wt (g)	48.00	47.42	54.33		54.58	51.08	(5)
	N Wt (g)	34.92	38.17	44.58		41.92	39.90	(5)
254	R Wt (g)	51.58	39.67		49.58	47.83	47.17	(1)
	S Wt (g)	66.33	53.75		70.50	62.17	63.19	(1)
	N Wt (g)	55.67	50.25		57.25	50.00	53.29	(1)
262	R Wt (g)	42.91		37.26	42.58	46.09	42.21	(3)
	S Wt (g)	61.42		53.08	58.75	62.25	58.88	(2)
	N Wt (g)	48.17		36.58	46.00	46.58	44.33	(4)
87	R Wt (g)		41.50	41.08	40.58	42.41	41.39	(4)
	S Wt (g)		57.42	55.67	61.00	52.50	56.65	(4)
	N Wt (g)		47.67	44.08	52.67	40.67	46.27	(3)
Mean and (Rank)	R Wt (g)	43.64 (2)	42.21 (4)	38.75 (5)	42.89 (3)	45.29 (1)	Pop Mean 42.56	
	S Wt (g)	58.23 (2)	53.59 (5)	54.63 (4)	62.54 (1)	57.88 (3)	Pop Mean 57.37	
	N Wt (g)	46.84 (2)	46.11 (3)	41.67 (5)	50.84 (1)	44.79 (4)	Pop Mean 46.05	

[a] Differences among means of crosses for dry weight of roots, stem and branches, and needles greater than 6.16, 6.94, and 7.37, respectively, are significant at 0.05 level, and greater than 7.83, 8.82, and 9.37 are significant at 0.01 level.

[b] Differences among means of female parents for dry weight of needles greater than 8.90 are significant at 0.05 level.

Table 9. Summary of analyses of variance for top and total dry weights

Source of Variation	Degrees of Freedom	Mean Squares	
		Top Dry Weight	Total Dry Weight
Replications	2	49.2667	311.4042
Treatments (T)	3	67,302.0819***	126,247.2930***
Crosses (C)	19	1,469.8901***	2,467.6480***
Female (F)	4	2,889.3027^{+}	4,248.1916
Male (M)	4	966.2507	1,513.7437
FxM	11	1,136.8816***	2,167.0519***
CxT	57	517.2749***	831.5737***
FxT	12	1,006.2314**	1,796.7287***
MxT	12	524.9432	816.6280
FxMxT	33	336.6840***	486.0431***
Residual	158	162.8869	255.2227
Total	239		

$^{+}$Significant at 0.10 level.

**Significant at 0.01 level.

***Significant at 0.005 level.

under the estimates of heritability for N in different parts of seedlings in the next section.

As in the case of other traits, there was a highly significant differential response to fertilizer treatments. Not only was the interaction of female x male x fertilizer treatment highly significant, but also the effect of female x fertilizer treatment interaction was strong (Table 9).

Mean values of crosses and general combining ability of parents for top and total dry weight are given in Table 10. The ranking of general combining ability of male parents was the same for top and total dry weights. However, the female parents failed to show such uniformity. Female parent 17, in particular, had a higher relative ranking in top dry weight than in total dry weight. This was due to the relatively low root development of crosses with this parent (Table 10).

Among the male parents, the highest amount of wood and foliage was produced by tree 98 (Table 10). However, the general combining ability of this parent for root dry weight was only third in ranking (Table 8). This means that a tree with the largest stem and foliage does not necessarily have the largest roots. In contrast, male parent 196, which ranked third in general combining ability for top and total dry weights, had the highest root growth (Tables 8 and 10). Notably, male parent 12, which had the lowest value of general combining ability for top and total dry weights, also had the lowest value for root dry weight (Tables 8 and 10).

Table 10. Mean of top dry weight (Top D Wt) and total dry weight (Total D Wt) of the crosses[a] and general combining ability of the parents[b]

FEMALE PARENTS		MALE PARENTS						
		1	5	12	98	196	Mean	(Rank)
17	Top D Wt (g)	105.75	104.08	96.84	107.34		103.50	(2)
	Total D Wt (g)	146.33	150.83	129.08	146.17		143.10	(4)
268	Top D Wt (g)	82.92	85.59	98.91		96.50	90.98	(5)
	Total D Wt (g)	122.42	126.48	143.33		141.33	133.39	(5)
254	Top D Wt (g)	122.00	104.00		127.75	112.17	116.48	(1)
	Total D Wt (g)	173.58	143.67		177.33	160.00	163.65	(1)
262	Top D Wt (g)	109.59		89.66	104.75	108.83	103.21	(3)
	Total D Wt (g)	152.50		126.92	147.33	154.92	145.42	(2)
87	Top D Wt (g)		105.09	99.75	113.67	93.17	102.92	(4)
	Total D Wt (g)		146.59	140.83	154.25	135.58	144.31	(3)
Mean and (Rank)	Top D Wt (g)	105.07 (2)	99.69 (4)	96.29 (5)	113.38 (1)	102.67 (3)	Pop Mean 103.42	
	Total D Wt (g)	148.72 (2)	141.89 (4)	135.04 (5)	156.27 (1)	147.96 (3)	Pop Mean 145.97	

[a] Differences among means of crosses for top and total dry weight greater than 12.78 and 16.00, respectively, are significant at 0.05 level, and greater than 16.25 and 20.33 are significant at 0.01 level.

[b] Differences among means of female parents for top dry weight greater than 16.49 are significant at 0.05 level.

Fertilizer treatments had a striking effect on top and total dry weights. Regardless of genetic effects and genotype x fertilizer treatment interactions, the highest average values were found for NP-treated seedlings. The lowest values for both traits belonged to seedlings grown with N fertilizer (Table 5).

Cross 254 x 98 had the highest top and total dry weight (Table 10). Both parents of this cross also had the highest general combining ability for most of the traits under investigation.

Fertilizer Treatments and Development of Seedlings

Direct observation on the development of seedlings showed that the fertilizer treatments had a marked effect on the needle development of terminal shoots. Seedlings grown with NP, developed needles earlier than their full-sibs or half-sibs under other fertilizer treatments. This was followed by seedlings treated with P, control, and N, respectively. On the average, the seedlings treated with P developed needles 3 days later than NP-treated seedlings. The time lag for controls was 7 days and for N-treated seedlings as long as 20 days.

Nitrogen and Phosphorus in Seedlings

Nitrogen Absorption and Its Translocation into Aerial Organs

In forest tree breeding, genotypes highly responsive to fertilizers may be distinguished on the basis of their ability to absorb and/or translocate nutrients effectively. While the physiological aspects of absorption and translocation were not the subject of this study, these terms were used to specify total N or P content of seedlings and total N or P content of aerial organs of seedlings, respectively.

There were highly significant differences in absorbed and translocated N among crosses (Table 11). Although there was some evidence of the effect of female parents, the cause of these differences was mostly female x male interaction.

Crosses also showed a significant differential response of absorbed and translocated N to applied fertilizers. This was shown by the significant effect of cross x fertilizer treatment interaction (Table 11). Further analysis showed that female x fertilizer treatment, male x fertilizer treatment, and female x male x fertilizer treatment interactions all had strong effects on variability of these traits (Table 11).

Female parent 254, which ranked first in general combining ability for N absorption, also produced two crosses (254 x 1 and 254 x 98) with the highest values for this trait (Table 12).

Ranking of general combining ability of parent trees for several characteristics is given in Table 13. Accordingly, the absorbed and translocated N in most cases ranked the same as top fresh and dry weights.

Nitrogen in Different Parts of Seedlings

To determine the nature of distribution of absorbed N in different parts of seedlings, the variation in accumulated N in roots, in stem and branches, and in needles was studied. The data provide information concerning the amount of N in different parts of seedlings, and their relationship with growth characteristics.

Table 11. Summary of analyses of variance for N absorption and translocation

Source of Variation	Degrees of Freedom		Mean Squares	
			N Absorption	N Translocation
Replications	2		3,633.2200	19,105.2875
Treatments (T)	3		26,481,560.9000***	14,101,221.0152***
Crosses (C)	19		127,121.2837***	92,194.0725***
Female (F)		4	226,643.5025^{+}	147,060.7993
Male (M)		4	142,224.1025	64,529.0076
FxM		11	85,439.4518***	82,302.5592***
CxT	57		111,087.5279***	74,441.5415***
FxT		12	177,870.4225***	103,904.5937**
MxT		12	207,842.1417***	82,896.7465*
FxMxT		33	51,619.3430*	35,114.9436***
Residual	158		32,442.0562	19,076.9372
Total	239			

$^{+}$Significant at 0.10 level.

*Significant at 0.05 level.

**Significant at 0.01 level.

***Significant at 0.005 level.

Table 12. Mean of N absorption (Abs) and translocation (Trans) of the crosses[a] and general combining ability of the parents[b]

		MALE PARENTS					
		1	5	12	98	196	Mean (Rank)
FEMALE PARENTS 17	Abs (mg)	1,595.7	1,548.4	1,421.0	1,529.6		1,523.68 (2)
	Trans (mg)	1,218.7	1,108.0	1,093.1	1,181.1		1,150.23 (1)
268	Abs (mg)	1,351.0	1,395.9	1,356.7		1,345.0	1,362.15 (5)
	Trans (mg)	895.6	1,018.2	1,079.5		967.7	990.25 (5)
254	Abs (mg)	1,653.9	1,490.3		1,626.1	1,567.7	1,584.50 (1)
	Trans (mg)	1,199.9	1,076.6		1,191.3	1,130.7	1,149.63 (2)
262	Abs (mg)	1,531.6		1,274.2	1,527.3	1,521.1	1,463.55 (3)
	Trans (mg)	1,123.4		968.3	1,169.0	1,142.1	1,100.70 (3)
87	Abs (mg)		1,456.8	1,440.8	1,537.9	1,399.9	1,458.85 (4)
	Trans (mg)		1,060.9	1,075.1	1,164.4	1,004.0	1,076.10 (4)
Mean and (Rank)	Abs (mg)	1,533.05 (2)	1,472.85 (3)	1,373.18 (5)	1,555.23 (1)	1,458.43 (4)	Pop Mean 1,478.55
	Trans (mg)	1,109.40 (2)	1,065.93 (3)	1,054.00 (5)	1,176.45 (1)	1,061.13 (4)	Pop Mean 1,093.38

[a] Differences among means of crosses for N absorption and translocation greater than 180.42 and 138.35, respectively, are significant at 0.05 level, and greater than 229.30 and 175.83 are significant at 0.01 level.

[b] Differences among means of female parents for N absorption greater than 143.02 are significant at 0.05 level.

Table 13. Ranking of general combining ability of female and male parents for different traits

	Parents	Absorption		Translocation		Needle Content		Top Weight	
		N	P	N	P	N	P	Fresh	Dry
FEMALE	17	2	2	1	2	1	3	2	2
	268	5	4	5	5	5	5	5	5
	254	1	1	2	1	2	1	1	1
	262	3	5	3	3	4	4	3	3
	87	4	3	4	4	3	2	4	4
	Range[a]	(1362-1584)[+]	(95-108)	(990-1150)	(65-76)	(660-803)	(35-42)	(290-350)	(91-116)[+]
MALE	1	2	2	2	2	2	2	2	2
	5	3	4	3	4	3	4	4	4
	12	5	5	5	5	5	5	5	5
	98	1	1	1	1	1	1	1	1
	196	4	3	4	3	4	3	3	3
	Range[a]	(1373-1555)	(90-104)	(1054-1176)	(65-75)	(721-806)	(35-40)	(305-342)	(96-113)

[a] Minimum and maximum values for absorption, translocation, and needle content are in mg and for top weight are in g.

[+] Significant difference at 0.10 level.

According to analysis of variance, the differences in N content of roots, stem and branches, and needles were highly significant among crosses (Table 14). In this respect, a significant effect of male parents on N content of stem and branches was noted (Table 14). However, most of the effects were caused by female x male interaction.

Like other traits discussed, there was a highly significant differential response with respect to N content of tissues among crosses (Table 14). This differential response was mainly due to the effect of female x male x fertilizer treatment interaction.

Mean values of crosses and general combining ability of parents for N in roots, stem and branches, and needles are given in Table 15. The ranking of general combining ability of parents for the above traits was inconsistent in most of the cases (Table 15). However, the ranking of general combining ability of male parents for N in needles was the same as those of N absorption and translocation (Table 13). Except for a few cases, this was also true for female parents (Table 13).

Phosphorus Absorption and Its Translocation into Aerial Organs

Differences in absorbed P and its translocation into the stem and foliage of the seedlings were highly significant among crosses (Table 16). While there was no significant effect of male or female parents, the female x male interaction was highly significant.

There were also highly significant effects of genotype x

Table 14. Summary of analyses of variance for N in roots, in stem and branches, and in needles

Source of Variation	Degrees of Freedom	Mean Squares		
		N in Roots	N in Stem and Branches	N in Needles
Replications	2	30,250.0000***	4,750.0000	27,850.0000
Treatments (T)	3	2,004,733.3333***	2,806,300.1133***	4,414,633.3333***
Crosses (C)	19	17,805.2632***	7,642.1053***	65,131.5789***
Female (F)	4	27,750.0000	8,575.0000	123,750.0000
Male (M)	4	16,725.0000	14,400.0000^{+}	21,350.0000
FxM	11	14,581.8182***	4,845.4545^{+}	59,736.3636***
CxT	57	16,563.1579***	6,715.7895***	52,761.4035***
FxT	12	21,475.0014^{+}	8,591.6667	68,325.0066
MxT	12	25,566.6667*	4,716.6667	68,391.6667
FxMxT	33	11,503.0303***	6,760.6061***	41,418.1818***
Residual	158	5,209.4937	2,910.7595	16,258.8608
Total	239			

$^{+}$Significant at 0.10 level.

*Significant at 0.05 level.

***Significant at 0.005 level.

Table 15. Mean of N in roots (R), in stem and branches (S), and in needles (N) of the crosses[a] and general combining ability of the parents[b]

FEMALE PARENTS		MALE PARENTS 1	5	12	98	196	Mean	(Rank)
17	R (mg)	377.0	455.3	327.9	348.5		377.18	(3)
	S (mg)	339.2	323.5	352.5	375.7		347.73	(3)
	N (mg)	879.5	784.5	740.6	805.5		802.53	(1)
268	R (mg)	455.4	377.7	277.2		377.3	371.90	(4)
	S (mg)	311.3	332.8	342.4		336.2	330.68	(4)
	N (mg)	584.3	685.4	737.1		631.5	659.58	(5)
254	R (mg)	454.0	413.7		434.8	437.0	434.88	(1)
	S (mg)	373.8	321.4		381.8	342.7	354.93	(1)
	N (mg)	826.1	755.2		809.5	788.0	794.70	(2)
262	R (mg)	408.2		305.9	358.3	379.0	362.85	(5)
	S (mg)	359.7		320.7	391.0	321.5	348.23	(2)
	N (mg)	763.7		647.6	778.0	820.6	752.48	(4)
87	R (mg)		395.9	365.7	373.5	395.9	382.75	(2)
	S (mg)		318.8	316.9	331.5	301.0	317.05	(5)
	N (mg)		742.1	758.2	832.9	703.0	759.05	(3)
Mean and (Rank)	R (mg)	423.65 (2)	410.65 (1)	319.18 (5)	378.78 (4)	397.30 (3)	Pop Mean 385.91	
	S (mg)	346.00 (2)	324.13 (5)	333.13 (3)	370.00 (1)	325.35 (4)	Pop Mean 339.72	
	N (mg)	763.40 (2)	741.80 (3)	720.88 (5)	806.48 (1)	735.78 (4)	Pop Mean 753.67	

[a] Differences among means of crosses for N in roots, in stem and branches, and in needles greater than 72.30, 54.04, and 127.73, respectively, are significant at 0.05 level, and greater than 91.88, 68.68, and 162.32 are significant at 0.01 level.

[b] Differences among means of male parents for N in stem and branches greater than 34.06 are significant at 0.05 level.

Table 16. Summary of analyses of variance for P absorption and translocation

Source of Variation	Degrees of Freedom	Mean Squares	
		P Absorption	P Translocation
Replications	2	156.5650	95.6535
Treatments (T)	3	$387,338.7867^{***}$	$209,218.7544^{***}$
Crosses (C)	19	783.0305^{***}	466.6353^{***}
Female (F)	4	1,051.8450	667.8256
Male (M)	4	1,060.7950	526.9969
FxM	11	584.2745^{***}	370.4892^{***}
CxT	57	381.3857^{***}	236.8681^{***}
FxT	12	662.6358^{*}	334.4799^{+}
MxT	12	472.4866^{+}	267.4987
FxMxT	33	245.9854^{***}	190.2345^{***}
Residual	158	103.1683	70.3983
Total	239		

$^{+}$Significant at 0.10 level.

*Significant at 0.05 level.

***Significant at 0.005 level.

fertilizer treatment interaction. This was due to female x fertilizer treatment, male x fertilizer treatment and female x male x fertilizer treatment interactions in the case of absorption and due to female x fertilizer treatment and female x male x fertilizer treatment interactions in the case of P translocation (Table 16).

Ranking of general combining ability of parents for P absorption was almost the same as translocation (Table 17). Female parent 254, which had the first rank for N absorption, also had the highest rank for P absorption and translocation. Among the male parents, tree 98, which had the highest general combining abilities for both N absorption and translocation, ranked first for P absorption and translocation (Table 13).

In general, there was a close, and in some cases exact, relationship between N and P absorption and their translocation into aerial organs, and growth characteristics on the basis of fresh and dry weight of top (Table 13).

Phosphorus in Different Parts of Seedlings

Variation among the accumulated P in roots, in stem and branches, and in needles was investigated. Summary of analyses of variance for these traits is given in Table 18. Accordingly, the cause of variation was mostly due to female x male and female x male x fertilizer treatment interactions. Except for the significant effect of male parents on P content of roots, the parents did not affect the P content of tissues significantly (Table 18).

Table 17. Mean of P absorption (Abs) and translocation (Trans) of the crosses[a] and general combining ability of parents

		MALE PARENTS						
		1	5	12	98	196	Mean	(Rank)
FEMALE PARENTS 17	Abs (mg)	100.0	95.4	90.8	100.6		96.70	(2)
	Trans (mg)	73.8	68.3	69.5	71.4		70.75	(2)
268	Abs (mg)	94.1	91.7	100.3		97.3	95.85	(4)
	Trans (mg)	63.8	61.1	69.9		65.3	65.05	(5)
254	Abs (mg)	111.1	100.7		118.5	103.4	108.43	(1)
	Trans (mg)	78.1	72.9		86.2	68.8	76.50	(1)
262	Abs (mg)	102.4		79.3	95.9	104.3	95.48	(5)
	Trans (mg)	74.1		58.0	69.1	71.4	68.15	(3)
87	Abs (mg)		93.2	91.7	101.0	100.0	96.48	(3)
	Trans (mg)		65.2	64.4	73.5	66.4	67.38	(4)
Mean and (Rank)	Abs (mg)	101.90 (2)	95.25 (4)	90.53 (5)	104.00 (1)	101.25 (3)	Pop Mean 98.59	
	Trans (mg)	72.45 (2)	66.88 (4)	65.45 (5)	75.05 (1)	67.98 (3)	Pop Mean 69.56	

[a] Differences among means of crosses for P absorption and translocation greater than 10.17 and 8.40, respectively, are significant at 0.05 level, and greater than 12.93 and 10.68 are significant at 0.01 level.

Table 18. Summary of analyses of variance for P in roots, in stem and branches, and in needles

Source of Variation	Degrees of Freedom	Mean Squares		
		P in Roots	P in Stem and Branches	P in Needles
Replications	2	67.7400	14.0000	95.3590^{+}
Treatments (T)	3	27,453.3400***	43,640.6667***	62,983.1260***
Crosses (C)	19	157.2184***	126.8421***	186.6498***
Female (F)	4	182.0475	118.5000	325.2412
Male (M)	4	302.2350^{+}	222.5000	87.7894
FxM	11	95.4564***	95.0909***	172.2022***
CxT	57	85.1540***	75.5439**	107.7308***
FxT	12	105.8250^{+}	96.5833	137.4461
MxT	12	122.7742^{+}	102.0833^{+}	116.7574
FxMxT	33	63.9573***	58.2424***	93.6426***
Residual	158	31.5742	16.7785	38.2135
Total	239			

$^{+}$Significant at 0.10 level.

**Significant at 0.01 level.

***Significant at 0.005 level.

Mean values of crosses and general combining ability of parents for the above traits are shown in Table 19. Except for a few cases, the ranking of general combining ability of parents was not the same for all of these traits.

Concentration of N and P in Tissue

Data for concentration of N and P (percent of N and P on the basis of tissue dry weight) in roots, stem and branches, and needles are given in Tables A-1 through A-6 in appendix. These data were used for calculation of total N and P in different parts of seedlings. Study of variability among the N and P concentration was not the subject of this investigation, and therefore no analyses were performed for these data.

Heritability Estimates

Heritability is defined as the proportion of total phenotypic variation attributable to genetic variations. In the present study, heritability for general adaptability (Dickerson, 1961) has been used to explain additive genetic variability in relation to phenotypic variability. Genes segregate and rejoin into new combinations exhibiting not only additive gene effects but also dominance and epistasis. Thus, in heritability for general adaptability only the additive portion is considered. This term is equivalent to narrow sense heritability, and was chosen because heritability estimate based on additive gene effects is a valid measure for a broad range of environments.

In contrast, the term heritability for local adaptability (Dickerson, 1961) was used to explain the proportion of both

Table 19. Mean of P in roots (R), in stem and branches (S) and in needles (N) of the crosses[a] and general combining ability of the parents[b]

			MALE PARENTS					
		1	5	12	98	196	Mean	(Rank)
FEMALE PARENTS								
17	R (mg)	26.2	27.1	21.3	29.2		25.95	(5)
	S (mg)	32.8	31.5	34.3	35.5		33.53	(2)
	N (mg)	41.0	36.8	35.1	35.9		37.20	(3)
268	R (mg)	30.3	30.6	30.4		32.0	30.83	(2)
	S (mg)	32.5	28.5	31.4		29.5	30.50	(4)
	N (mg)	31.3	32.6	38.5		35.8	34.55	(5)
254	R (mg)	33.0	27.8		32.3	34.6	31.93	(1)
	S (mg)	36.3	29.3		39.9	30.9	34.13	(1)
	N (mg)	41.8	43.6		46.3	37.9	42.38	(1)
262	R (mg)	28.3		21.3	26.8	32.9	27.33	(4)
	S (mg)	36.5		27.9	31.3	32.7	32.10	(3)
	N (mg)	37.6		30.1	37.8	38.7	36.03	(4)
87	R (mg)		28.0	27.3	27.5	33.6	29.10	(3)
	S (mg)		28.4	28.4	32.0	28.9	29.43	(5)
	N (mg)		36.8	36.0	41.5	37.5	37.95	(2)
Mean and (Rank)	R (mg)	29.45 (2)	28.38 (4)	25.08 (4)	28.95 (3)	33.28 (1)	Pop Mean 29.03	
	S (mg)	34.53 (2)	29.43 (5)	30.50 (3,4)	34.68 (1)	30.50 (3,4)	Pop Mean 31.93	
	N (mg)	37.93 (2)	37.45 (4)	34.93 (5)	40.38 (1)	37.48 (3)	Pop Mean 37.62	

[a] Differences among means of crosses for P in roots, in stem and branches, and in needles, greater than 5.63, 4.10, and 6.19,respectively, are significant at 0.05 level, and greater than 7.15, 5.21, and 7.87 are significant at 0.01 level.

[b] Differences among means of male parents for P in roots greater than 4.78 are significant at 0.05 level.

additive genetic and genotype x environment interaction components in relation to phenotypic variability. It is a valid measure to test the traits under an environmental condition similar to that of the experimental condition. This heritability is not the same as broad sense heritability and is applicable when genotype x environment interactions are present and can be taken advantage of by selection for particular environmental conditions.

Estimates of Heritability for Height and Diameter Growth

Heritability estimates for height and diameter growth were made using the estimates of components of variance in Table 20 and the heritability formulae on pages 24 and 25. For each trait, heritability estimates for general adaptability (GA), and local adaptability (LA) were calculated (Table 21). Heritability estimates were determined for male, female, and their combination (male + female). According to Falconer (1960) the two estimates, from the female and male parents, are equally reliable, and their combination may be taken as the best estimate of heritability.

Heritability estimates for height and diameter growth were found to be moderate under general adaptability. For example, 31.4 percent of the phenotypic variability in height growth was due to additive genetic effects. This means that the breeder should expect a gain of 31.4 percent of selection differential for height growth in the next generation. The value for diameter growth was smaller than that of height growth. Much greater gain is expected under local adaptability.

Table 20. Estimates of components of variance for height and diameter growth

Source	Height Growth	Diameter Growth[a]
Female (F)	8.1889	0.0013
Male (M)	6.4300	0.1781
FxM	21.0592	0.1825
FxT[b]	-1.3579	-0.0219
MxT	6.5668	0.0619
FxMxT	34.4880	0.2850
Error	53.2037	2.0500
Phenotypic Variance[c]	93.1097	1.3702

[a] Values multiplied by 10^2

[b] T = fertilizer treatment

[c] See page 25 for components of phenotypic variance.

Table 21. Heritability estimates and the magnitude of interaction components for height and diameter growth

Components[a]	Height Growth		Diameter Growth	
	GA[b]	LA[c]	GA[b]	LA[c]
		HERITABILITY ESTIMATES		
h^2_F	0.352	0.778	0.004	0.241
h^2_M	0.276	0.702	0.520	0.757
h^2_{F+M}	0.314	0.740	0.262	0.499
		INTERACTION COMPONENTS		
σ^2_{FxM}	23	-	13	-
σ^2_{FxMxT}	37	-	21	-
σ^2_{GxT}	43	-	24	-

[a] Values for interaction components are in percent of phenotypic variance. For symbols see pages 22 and 25.

[b] General adaptability as defined on page 25.

[c] Local adaptability as defined on page 25.

The magnitude of nonadditive genetic and nonadditive genetic x fertilizer treatment interactions was also determined (Table 21). For each trait the magnitude of interaction components was calculated in percent of phenotypic variance. The data showed that a high portion of the phenotypic variability was due to genotype x fertilizer treatment interaction.

Estimates of Heritability for Weight Characteristics

Information concerning the inheritance of root growth, stems and branches, and needles is useful. For example, root growth may be a significant factor in developing genotypes with characteristics of drought resistance for dry sites. It could be important in breeding trees for areas exposed to high winds. In species that root growth proved to be correlated with tree growth, it could be used as a growth index.

Plants' photosynthetic processes occur in chloroplasts of their leaves. One may consider the efficiency of photosynthesis on the basis of the relationship between needle weight and/or crown area and tree growth. Thus, the study of inheritance of needle weight is of biological importance in tree breeding.

Estimates of heritability for dry weight of roots, stem and branches, and needles were made using the component estimates of Table 22. The heritabilities of these traits were determined for both general and local adaptability (Table 23). Negative values were found for root dry weight under general adaptability (Table 23). This means that variation of root dry weight of different crosses was not related to additive gene effects. As

Table 22. Estimates of components of variance for dry weight of roots, stem and branches, and needles

Source	Roots	Stem and Branches	Needles
Female (F)	-0.1588	7.6995	10.5546
Male (M)	-2.1013	1.0404	-1.7372
FxM	19.0570	20.5306	23.0678
FxT[a]	4.6662	9.4615	10.7731
MxT	3.7814	-0.9020	5.6327
FxMxT	6.4192	21.2758	8.5384
Error	37.8128	48.0112	54.2358
Phenotypic Variance[b]	44.2681	75.1095	74.9080

[a] T = fertilizer treatment

[b] See page 25 for components of phenotypic variance.

Table 23. Heritability estimates and the magnitude of interaction components for dry weight of roots, stem and branches, and needles

Components[a]	Roots		Stem and Branches		Needles	
	GA[b]	LA[c]	GA[b]	LA[c]	GA[b]	LA[c]
			HERITABILITY ESTIMATES			
h^2_F	-0.012	0.321	0.410	0.807	0.564	0.897
h^2_M	-0.190	0.146	0.055	0.453	-0.093	0.426
h^2_{F+M}	-0.101	0.233	0.208	0.630	0.236	0.661
			INTERACTION COMPONENTS			
σ^2_{FxM}	43	-	27	-	31	-
σ^2_{FxMxT}	15	-	28	-	11	-
σ^2_{GxT}	34	-	40	-	33	-

[a] Values for interaction components are in percent of phenotypic variance. For symbols see pages 22 and 25.

[b] General adaptability as defined on page 25.

[c] Local adaptability as defined on page 25.

was shown by analysis of variance (Table 7), the variation was due to fertilizer treatments, female x male, and genotype x fertilizer treatment interactions. The effect of fertilizer treatment was so high that it could have masked the possible low additive genetic variation among the roots.

The magnitude of interaction components is also shown in Table 23. These values are in percent of phenotypic variance. Highest value for total interaction effects was obtained for root dry weight with the lowest value for needles. This indicates less genetic variation in roots than needles in sample population.

Heritability estimates for fresh and dry weight of top and for total dry weight of seedlings were determined. For this purpose, the genetic components of variance, listed in Table 24, were used. Heritability values and magnitude of interaction components are given in Table 25.

Estimates of combined heritability for top fresh weight were similar to that of top dry weight (Table 25). However, the corresponding heritability for total dry weight of seedlings was much smaller. This was considered to be due to the incorporation of nonadditive genetic components of root dry weight in the total dry weight components.

Highest magnitude of interaction components was obtained for total dry weight and the lowest value was associated with top fresh weight (Table 25). In all traits a considerable portion of phenotypic variability was caused by the genotype x fertilizer treatment interaction component.

Table 24. Estimates of components of variance for top fresh and dry weight, and the total dry weight of seedlings

Source	Top Fresh Weight	Top Dry Weight	Total Dry Weight
Female (F)	213.9237	36.5088	43.3570
Male (M)	-45.3322	-3.5548	-13.6105
FxM	456.2095	81.1662	159.3191
FxT[a]	137.0495	41.8467	81.9178
MxT	21.4720	11.7662	20.6615
FxMxT	217.0565	43.4493	57.7051
Error	1,606.2375	162.8869	255.2227
Phenotypic Variance[b]	1,535.7914	265.4780	434.4242

[a] T = fertilizer treatment

[b] See page 25 for components of phenotypic variance.

Table 25. Heritability estimates and the magnitude of interaction components for top fresh and dry weight, and total dry weight

Components[a]	Top Fresh Weight		Top Dry Weight		Total Dry Weight	
	GA[b]	LA[c]	GA[b]	LA[c]	GA[b]	LA[c]
	HERITABILITY ESTIMATES					
h^2_F	0.557	0.802	0.550	0.916	0.399	0.768
h^2_M	-0.118	0.126	-0.054	0.312	-0.125	0.244
h^2_{F+M}	0.220	0.464	0.230	0.614	0.137	0.506
	INTERACTION COMPONENTS					
σ^2_{FxM}	30	-	31	-	37	-
σ^2_{FxMxT}	14	-	16	-	13	-
σ^2_{GxT}	24	-	37	-	37	-

[a] Values for interaction components are in percent of phenotypic variance. For symbols see pages 22 and 25.

[b] General adaptability as defined on page 25.

[c] Local adaptability as defined on page 25.

Estimates of Heritability for N Absorption and Translocation

Breeders need to distinguish fertilizer-responsive genotypes for selection. Genotypes can be selected on the basis of their physical response to fertilizers. However, if the response was completely environmental the progenies of the selected parents may show no improvement in response to fertilizers. Thus, the response of trees to fertilizers should be analyzed in terms of absorption and/or translocation of nutrients into aerial organs and on the basis of correlation of these traits with growth characteristics. Therefore, if a fertilizer-responsive genotype grows well because (a) it has greater ability to absorb and translocate nutrients (b) because the processes of absorption and translocation are inherited and (c) because the genetic correlations between these traits and growth characteristics are high, then this genotype should produce fertilizer-responsive progenies. Here, the degree of inheritance (heritability estimates) of the above traits and their correlation with growth characteristics are the important factors in estimation of genetic gain.

Heritability estimates of N absorption and its translocation into aerial organs were determined using the estimates of genetic components in Table 26.

Heritability estimates for these traits were similar for female parents under general adaptability (Table 27). However, estimates of heritability for male parents were negative in the case of translocation and positive in the case of absorption (Table 27).

Table 26. Estimates of components of variance for N absorption and translocation

Source	N Absorption	N Translocation
Female (F)	2,941.7511	1,349.1300
Male (M)	1,183.0136	-370.2823
FxM	4,416.4496	5,268.8018
FxT[a]	7,890.6925	4,299.3531
MxT	9,763.9249	2,986.3627
FxMxT	4,794.3217	4,009.5016
Error	32,442.0562	19,076.9372
Phenotypic Variance[b]	41,804.1721	23,901.8460

[a] T = fertilizer treatment

[b] See page 25 for components of phenotypic variance.

Table 27. Heritability estimates and the magnitude of interaction components for N absorption and translocation

Components[a]	N Absorption GA[b]	N Absorption LA[c]	N Translocation[d] GA[b]	N Translocation[d] LA[c]
		HERITABILITY ESTIMATES		
h^2_F	0.281	0.818	0.226	0.698
h^2_M	0.113	0.650	-0.062	0.411
h^2_{F+M}	0.197	0.734	0.082	0.554
		INTERACTION COMPONENTS		
σ^2_{FxM}	11	-	22	-
σ^2_{FxMxT}	12	-	17	-
σ^2_{GxT}	54	-	47	-

[a] Values for interaction components are in percent of phenotypic variance. For symbols see pages 22 and 25.

[b] General adaptability as defined on page 25.

[c] Local adaptability as defined on page 25.

[d] Translocated N in stem, branches, and needles.

The negative value was due to the effect of the male component of variance for N content of needles. (See discussion on heritability of N in different parts of seedlings.) As a result, the combined heritabilities of translocation were much smaller than those of absorption.

The magnitude of the female x male interaction component for translocation of N in stem and foliage was twice as high as that for absorption. This was also considered to be due to the negative effect of male parents for N content of needles.

Estimates of Heritability for N in Different Parts of Seedlings

The components of variance in Table 28 were used to calculate heritabilities of the above traits. These heritability estimates are given in Table 29.

A relatively low heritability (combined) under general adaptability was estimated for N in needles. This resulted from the negative heritability of the male parents. In contrast, the heritability of this trait was relatively high for the female parents. There was no reason to believe that in a population of pine trees there was a real difference in mode of inheritance between male and female parents. The negative heritability for N content of needles could result from sampling variation. Or this could be simply due to the loss of some needles from a few seedlings which was noticed during the course of the experiment. On several occasions portions of the needles of a few seedlings were found dead for unknown reasons.

The usual high magnitude of interaction components was found

Table 28. Estimates of components of variance for N in roots, stem and branches, and needles

Source	N in Roots	N in Stem and Branches	N in Needles
Female (F)	274.3371	77.6989	1,333.6174
Male (M)	44.6496	199.0530	-459.7159
FxM	781.0270	161.2246	3,623.1252
FxT[a]	623.2481	114.4413	1,681.6761
MxT	878.9773	-127.7462	1,704.5928
FxMxT	1,573.3842	962.4617	6,289.8303
Error	5,209.4979	970.2532	16,258.8608
Phenotypic Variance[b]	5,912.1212	2,357.3856	19,602.7461

[a] T = fertilizer treatment

[b] See page 25 for components of phenotypic variance.

Table 29. Heritability estimates and the magnitude of interaction components for N in roots, stem and branches, and needles

	N in Roots		N in Stem and Branches		N in Needles	
Components[a]	GA[b]	LA[c]	GA[b]	LA[c]	GA[b]	LA[c]
			HERITABILITY ESTIMATES			
h^2_F	0.186	0.706	0.132	0.535	0.272	0.766
h^2_M	0.030	0.550	0.338	0.740	-0.092	0.340
h^2_{F+M}	0.108	0.628	0.235	0.638	0.090	0.583
			INTERACTION COMPONENTS			
σ^2_{FxM}	13	-	7	-	18	-
σ^2_{FxMxT}	27	-	41	-	32	-
σ^2_{GxT}	52	-	40	-	49	-

[a] Values for interaction components are in percent of phenotypic variance. For symbols see pages 22 and 25.

[b] General adaptability as defined on page 25.

[c] Local adaptability as defined on page 25.

for the above traits. Genotype x fertilizer treatment interaction was highest for accumulated N in roots. But the magnitude of total interaction components was highest for N in needles (Table 29).

Estimates of Heritability for P Absorption and Translocation

Using the estimates of components of variance in Table 30, the heritabilities for P absorption and translocation were determined (Table 31).

The heritability estimates for these traits were higher than those of N absorption and translocation. But, none of these traits had high heritability under general adaptability (above 0.50).

In general, heritability estimates for N and P in whole or parts of seedlings were on the order of heritability of diameter growth. Regarding the present procedure of forest tree breeding, with the idea of breeding for broad range of environment, some of the heritability estimates are considered to be low. However, if for each specific environment suitable genotypes are developed, the respective heritabilities are high.

Estimates of Heritability for P in Different Parts of Seedlings

In addition to heritability estimates for P absorption and translocation, the heritability estimates for accumulated P in roots, in stem and branches, and in needles were determined separately. The data of Table 32 were used for this purpose. Estimates of heritability for general and local adaptability of the above traits are given in Table 33. Due to the negative value of the component of variance for P in needles for male parents, the combined heritability estimate for this trait was much smaller

Table 30. Estimates of components of variance for P absorption and translocation

Source	P Absorption	P Translocation
Female (F)	9.7411	6.1945
Male (M)	9.9275	3.2606
FxM	40.0922	25.0076
FxT[a]	26.0407	9.0153
MxT	14.1563	4.8290
FxMxT	35.7043	29.9591
Error	103.1683	70.3983
Phenotypic Variance[b]	170.0515	101.7322

[a] T = fertilizer treatment

[b] See page 25 for components of phenotypic variance.

Table 31. Heritability estimates and the magnitude of interaction components for P absorption and translocation

Components[a]	P Absorption		P Translocation[d]	
	GA[b]	LA[c]	GA[b]	LA[c]
	HERITABILITY ESTIMATES			
h^2_F	0.229	0.676	0.244	0.674
h^2_M	0.233	0.680	0.128	0.559
h^2_{F+M}	0.231	0.678	0.186	0.616
	INTERACTION COMPONENTS			
σ^2_{FxM}	24	-	25	-
σ^2_{FxMxT}	21	-	29	-
σ^2_{GxT}	45	-	43	-

[a] Values for interaction components are in percent of phenotypic variance. For symbols see pages 22 and 25.

[b] General adaptability as defined on page 25.

[c] Local adaptability as defined on page 25.

[d] Translocated P in stem, branches and needles

Table 32. Estimates of components of variance for P in roots, stem and branches, and needles

Source	P in Roots	P in Stem and Branches	P in Needles
Female (F)	1.8040	0.4773	3.1883
Male (M)	4.3079	2.6544	-1.7586
FxM	5.3235	6.5260	11.1657
FxT[a]	2.6167	2.3963	2.7377
MxT	3.6761	2.7401	1.4474
FxMxT	8.0958	10.3660	13.8572
Error	31.5742	16.7785	38.2135
Phenotypic Variance[b]	36.3487	30.7529	43.3755

[a] T = fertilizer treatment

[b] See page 25 for components of phenotypic variance.

Table 33. Heritability estimates and the magnitude of interaction components for P in roots, stem and branches, and needles

Components[a]	P in Roots		P in Stem and Branches		P in Needles	
	GA[b]	LA[c]	GA[b]	LA[c]	GA[b]	LA[c]
			HERITABILITY ESTIMATES			
h^2_F	0.199	0.594	0.062	0.566	0.301	0.710
h^2_M	0.474	0.870	0.345	0.849	-0.160	0.251
h^2_{F+M}	0.337	0.732	0.204	0.708	0.070	0.480
			INTERACTION COMPONENTS			
σ^2_{FxM}	15	-	21	-	16	-
σ^2_{FxMxT}	22	-	34	-	32	-
σ^2_{GxT}	40	-	50	-	25	-

[a] Values for interaction components are in percent of phenotypic variance. For symbols see pages 22 and 25.

[b] General adaptability as defined on page 25.

[c] Local adaptability as defined on page 25.

than that of other heritabilities (Table 33). The possible causes of this factor were explained earlier under the discussion of heritability for N in different parts of seedlings.

Genetic Correlation

Genetic correlation explains the property of a gene that affects two or more traits simultaneously (Falconer, 1960) or it may be considered to be the result of linked genes. Therefore, when the gene or block of genes affecting several traits was segregated it would cause simultaneous variation in respective traits. Negative genetic correlation is obtained when the traits are influenced by the same genes but in two opposite directions. Falconer (1960) considered genetic correlation as the correlation of breeding values.

In breeding programs, when the genetic correlation between two traits is high, selection for one of the traits can be carried out on the basis of the other trait. This is important in the case where one of the traits can be evaluated much earlier or easier, than the other. In this case, breeders can select for the trait which needs long-term evaluation on the basis of other traits which can be readily evaluated in an early stage of program.

It is clear that forest tree breeding is a long-term practice. A pine breeder not only waits two years to obtain the experimental seeds, he must also wait for a longer period of time (6-8 years) before selection in the new generation. Thus, a tree breeder needs some way of reducing the period of breeding for each trait. While it is not possible to give a definite answer to this problem at this stage, it seems that traits such as nutrient absorption and/or translocation, needle content, or some kind of biochemical reactions in seedlings may be a possible answer if (a) heritability estimates for traits such as nutrient absorption and/or translocation or needle content are not too low, (b) genetic correlation between these traits and those of growth characteristics are high, and (c) the growth of seedlings at the early stage (2-3 years old) are genetically correlated with that at maturity.

Traits such as nutrient absorption, translocation, or mineral content of needles in slash pine were proved to be inherited to some degree, and, therefore, can be used in selection programs. The above traits can be studied by tissue analysis at an early stage of tree development and in a short period of time. Therefore, these characteristics may be used as growth-determining factors in selection programs, if conditions in (b) and (c) above are satisfied. As a result, progeny tests may be shortened through tissue analysis of seedlings (or at least supplemented by additional information), and second or later generation selections may be accelerated by this procedure.

In order to determine the genetic correlation between traits such as absorption, translocation, and needle content, and those of growth characteristics, the components of covariance in Tables 34, 35, and 36 and the genetic correlation formula on page 26 were used. The additive genetic covariance was calculated on the basis of average value of female and male components of covariance. According to Falconer (1960), the component of female, male or

Table 34. Estimates of components of covariance for N absorption, translocation, and growth characteristics

Traits		Cov_{XY}		$Cov_{A_{XY}}$
X	Y	Female	Male	
N Absorption	N translocation	2,065.8695	263.9792	4,659.6974
	N in needles	1,697.9450	-71.1867	3,253.5168
	Height growth	164.0544	99.5856	527.2799
	Diameter growth	0.3918	-0.6860	-0.5855
	Top dry weight	322.9778	70.9105	787.7766
	Total dry weight	331.8686	73.6795	811.0962
N Translocation	Height growth	145.9077	78.3801	448.5756
	Diameter growth	-0.0762	-0.2466	-0.6456
	Top dry weight	192.2814	-3.8031	376.9566
	Total dry weight	169.0670	-34.1543	269.8253
N in Needles	Height growth	167.4575	33.1277	401.1704
	Diameter growth	-0.0218	-0.1721	-0.3878
	Top dry weight	214.9444	-43.5215	342.8458
	Total dry weight	181.7720	-73.8101	215.9238

Table 35. Estimates of components of covariance for P absorption, translocation, and growth characteristics

Traits		Cov_{XY}		$Cov_{A_{XY}}$
X	Y	Female	Male	
P Absorption	P translocation	6.8372	4.9582	23.5908
	P in needles	5.7577	1.7064	14.9282
	Height growth	3.4675	6.7498	20.4347
	Diameter growth	0.0014	-0.0254	-0.0480
	Top dry weight	17.1472	10.4617	55.2178
	Total dry weight	22.3959	13.8222	72.4361
P Translocation	Height growth	6.0330	7.6037	27.2735
	Diameter growth	0.0021	-0.0139	-0.0236
	Top dry weight	16.5572	6.5197	46.1537
	Total dry weight	19.7197	6.7538	52.9471
P in Needles	Height growth	4.8806	2.1881	14.1373
	Diameter growth	-0.0131	-0.0267	-0.0797
	Top dry weight	12.9393	-0.7296	24.4195
	Total dry weight	15.8867	-1.0442	29.6850

Table 36. Estimates of components of covariance for N and P absorption, translocation, needle content, and growth characteristics

Traits		Cov_{XY}		$Cov_{A_{XY}}$
X	Y	Female	Male	
N Absorption	Top Fresh Weight	810.7936	118.8387	1,859.2646
	Stem and Branches Dry Weight	151.0589	30.6762	363.4702
	Needles Dry Weight	171.4614	39.7769	422.4767
N Translocation	Top Fresh Weight	632.1355	548.4647	2,361.2005
	Stem and Branches Dry Weight	132.7789	136.4128	538.3833
	Needles Dry Weight	127.6354	115.2825	485.8359
N in Needles	Top Fresh Weight	507.1390	-119.2855	775.7069
	Stem and Branches Dry Weight	106.3027	-14.1226	184.3603
	Needles Dry Weight	105.4748	-30.3114	150.3268
P Absorption	Top Fresh Weight	40.3431	14.8802	110.4466
	Stem and Branches Dry Weight	6.9894	6.0568	26.0924
	Needles Dry Weight	10.1430	4.3733	29.0326
P Translocation	Top Fresh Weight	40.7287	11.4304	104.3182
	Stem and Branches Dry Weight	9.1645	4.2776	26.8842
	Needles Dry Weight	9.1042	2.6848	23.5780
P in Needles	Top Fresh Weight	28.4954	-4.3477	48.2954
	Stem and Branches Dry Weight	5.9737	0.0796	12.1067
	Needles Dry Weight	6.9438	-0.8215	12.2447

average component of male and female covariance of half-sibs estimates one-quarter of additive genetic covariance.

The additive genetic variance, used in calculation of genetic correlations, was also determined on the basis of average value of the female and male components of variance. The average of these two components was also considered to estimate one-quarter of additive genetic variance for half-sibs (Falconer, 1960).

There were comparatively high genetic correlations between N and P absorption, translocation, and needle content and growth characteristics (Table 37).

In contrast, the genetic correlations between N and P absorption, translocation, and needle content and the diameter growth were all negative. It appeared that the genes (or gene) affecting the absorption and/or translocation of nutrients were not the same as those affecting the diameter growth. This was not surprising because of the fact that the tallest seedlings did not have the greatest diameter in this experiment. It should be noted here that the genetic cause of correlation is chiefly through the pleiotropic action of genes (Falconer, 1960). Thus, the correlation resulting from pleiotropy explains the net effect of all the segregating genes that influence both traits (Falconer, 1960). Therefore, in one case some genes may increase one trait but others decrease the other traits. In this case a negative correlation will be obtained, even though both traits were affected by the same genes. Consequently, height and diameter growth, or absorption and translocation and diameter growth, could possibly be influenced by the same genes but in different directions.

Table 37. Genetic correlations for N and P absorption, translocation, and needle content and the growth characteristics

	Height Growth	Diameter Growth	Top Fresh Weight	Top Dry Weight	Stem and Branches Dry Weight	Needle Dry Weight	Total Dry Weight
Nitrogen Absorption	1.07	-0.10	1.12	1.03	0.96	1.11	1.16
Nitrogen Translocation	1.88	-0.24	2.91	1.05	2.91	2.62	0.79
Nitrogen in Needles	1.78	-0.16	1.01	1.01	1.06	0.86	0.67
Phosphorus Absorption	0.60	-0.13	0.96	1.29	1.00	1.10	1.50
Phosphorus Translocation	1.16	-0.09	1.31	1.30	1.48	1.29	1.58
Phosphorus in Needles	1.55	-0.79	1.56	1.78	1.71	1.72	2.28
Height Growth	-	-0.52	-	-	-	-	-

Genetic correlations between N and P absorption, translocation, and needle content were estimated. The correlations between these traits were also found to be positively significant (Table 38).

The results of correlation tests suggest that the nutrient absorption and/or their translocation into aerial organs of slash pine seedlings can be considered as an index of growth characteristics, based on top and total dry weight, stem and branches dry weight, top fresh weight, and height growth.

No genetic correlations were calculated for root growth with regard to other traits. This was due to the negative components of variance for male and female obtained for root growth (Table 22). Obviously, negative values could not be used in the genetic correlation formula.

Table 38. Genetic correlation between absorption, translocation, and needle content

	Translocation		Needle Content	
	N	P	N	P
Nitrogen Absorption	1.16	-	0.86	-
Phosphorus Absorption	-	0.87	-	1.41

RESULTS OF ^{33}P EXPERIMENT

The objective of this experiment was to determine the genetic differences in incorporation of phosphate into acid-soluble, nucleic acid and phospholipid-phosphoprotein fractions and to investigate the relationship between phosphate incorporation, substrate nutrient supply, and growth characteristics. Correlation between incorporation of phosphate into organic compounds and growth characteristics can be useful in selecting fast growing genotypes at an early stage of development. However, additional information concerning correlation between growth characteristics at different stages of maturity in slash pine is needed.

Phosphate Fractions in Roots

The percent incorporation of phosphate into acid-soluble fraction in high phosphate seedlings (seedlings treated with 50 to 100 ppm of P) was much higher than that in low phosphate seedlings (seedlings treated with 1 to 5 ppm of P)(Table 39). The lowest value was found in seedlings grown on 1 ppm of P.

The percent incorporation of phosphate into nucleic acid and phospholipid-phosphoprotein fractions was lower in high phosphate seedlings and much higher in low phosphate seedlings. Seedlings treated with 1 ppm of P had the highest nucleic acid fraction (Table 39). There was high variation in phosphate fractions in seedlings grown under different fertilizer treatments. However, the variation among lines for different fractions was much less (Fig. 6).

Table 39. Percent incorporation of P into acid-soluble (AS), nucleic acid (NA), and phospholipid-phosphoprotein (PL) fractions

Lines	P Fractions	Treatments				
		$N_{100}P_{50}$	$N_{50}P_{50}$	$N_{10}P_{1}$	$N_{50}P_{5}$	$N_{50}P_{100}$
		Percent of Total				
17	AS	81	82	43	53	81
	NA	13	10	35	21	15
	PL	6	8	22	26	4
254	AS	76	74	40	57	80
	NA	15	14	37	20	14
	PL	9	12	23	23	6
268	AS	74	73	53	58	77
	NA	13	16	30	20	16
	PL	13	11	18	22	7

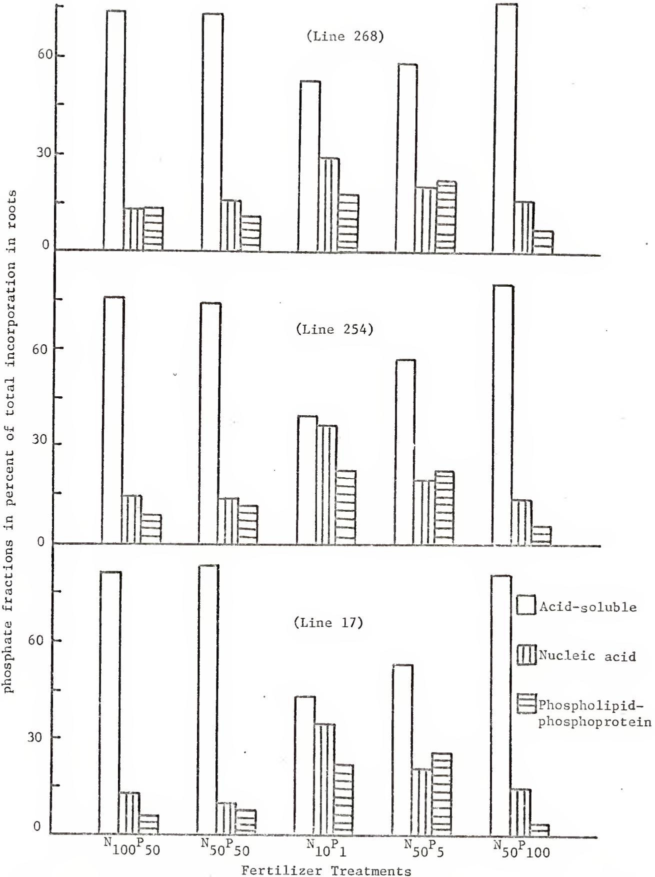

Fig. 6. Relative incorporation of phosphate into acid-soluble, nucleic acid, and phospholipid-phosphoprotein fractions in different lines.

The specific activity of phosphate incorporation into different fractions was also determined (Table 40). Different levels of P had marked effects on incorporation of phosphate into all three fractions. For example, when 50 and 100 ppm of P were applied in combination with 50 ppm of N, the incorporation of phosphate into all fractions was changed to a great extent. Except for one case, the specific activity of all phosphate fractions, in 3 lines, was lower in seedlings grown with 50 ppm of N and 100 ppm of P than those treated with 50 ppm of N and 50 ppm of P (Table 40).

Incorporation of phosphate into different fractions was also different in seedlings treated with different amount of nutrients but with the same ratio of N/P (treatments $N_{10}P_1$ and $N_{50}P_5$ both with N/P ratio of 10). In all cases, seedlings grown on 1 ppm of P showed much higher incorporation of phosphate into all fractions in root tissue (Table 40).

Different levels of N, applied with 50 ppm of P, influenced the rate of incorporation of phosphate into acid-soluble fraction differentially. In lines 254 and 268, the higher level of N stimulated the incorporation of phosphate, while in line 17, N depressed incorporation of phosphate into acid-soluble fraction (Table 40).

Differences in phosphate incorporation among lines were highly significant. Line 17 showed higher average (average over-all treatments) incorporation of phosphate into acid-soluble, nucleic acid, and phospholipid-phosphoprotein fractions than the other lines (Tables 40 and 41).

Table 40. Mean specific activity of P incorporation into acid-soluble (AS), nucleic acid (NA), and phospholipid-phosphoprotein (PL) fractions in roots

Lines	Fractions	Treatments $N_{100}P_{50}$	$N_{50}P_{50}$	$N_{10}P_1$	$N_{50}P_5$	$N_{50}P_{100}$	Mean[a]	(Rank)
		Mean Specific Activity of Three Seedlings (cpm/g)[b]						
17	AS	121,283	132,887	612,507	273,694	101,782	248,430	(1)
	NA	19,386	16,549	509,947	111,879	18,864	135,325	(1)
	PL	7,475	11,089	298,810	126,497	3,571	89,488	(1)
254	AS	145,098	116,709	506,571	214,890	94,326	215,519	(2)
	NA	28,428	22,108	467,086	75,625	16,680	121,985	(2)
	PL	15,912	17,383	284,169	81,406	5,630	80,900	(2)
268	AS	110,897	102,456	647,850	180,560	69,427	214,238	(3)
	NA	20,519	23,072	363,422	62,860	14,564	96,888	(3)
	PL	16,712	13,812	219,353	66,900	5,815	64,518	(3)
Mean[c]	AS	125,759	117,350	588,976	223,048	88,511		
	NA	22,778	20,576	446,818	83,454	16,702		
	PL	13,366	14,094	267,444	91,601	5,005		

[a] Differences among means of acid-soluble P, nucleic acid P, and phospholipid-phosphoprotein of lines greater than 13,572, 22,964, and 9,287, respectively, are significant at 0.05 level, and greater than 18,126, 30,670, and 12,403 are significant at 0.01 level.

[b] Differences among means of acid-soluble P, nucleic acid P, and phospholipid-phosphoprotein of lines within treatments greater than 34,242, 57,938, and 23,431, respectively, are significant at 0.05 level, and greater than 45,723, 77,364, and 31,287 are significant at 0.01 level.

[c] Differences among means of acid-soluble P, nucleic acid P, and phospholipid-phosphoprotein in different treatments greater than 18,444, 31,207, and 12,620, respectively, are significant at 0.05 level, and greater than 24,323, 41,155, and 16,643 are significant at 0.01 level.

Table 41. Summary of analysis of variance for different P fractions in roots, acid-soluble P in terminal shoots, and growth characteristics

Source of Variation	Degrees of Freedom	Mean Squares					
		Acid-Soluble Fraction[a]	Nucleic Acid Fraction[a]	Phospholipid-Phosphoprotein Fraction[a]	Terminal Shoots (Acid-Soluble) Fraction[a]	Height Growth	Top Fresh Weight
Treatments (T)	t-1 = 4	393,501**	310,802**	111,742**	483**	89.1152**	3.7834**
Lines (L)	(f-1) = 2	4,361**	5,713**	2,414**	359**	21.1460*	0.1455
LxT	(f-1)(t-1) = 8	5,714**	3,344**	1,490**	185**	2.1274	0.0223
Error (n-1)ft	30	299	856	140	13	5.1920	0.0900
n=3=seedlings/Family/pot=fxt.							
Total	44						

[a] Values are divided by 10^6 and rounded to nearest number.

[*] Significant at 0.05 level.

[**] Significant at 0.01 level.

Line x fertilizer treatment (LxT) interactions were highly significant for all phosphate fractions. This indicates differential response of seedlings to fertilizer treatments (Table 41). Differential responses can also be seen from the data in Table 40. For example, incorporation of phosphate into each of the three fractions in line 17 was much higher than in line 254 under $N_{50}P_5$. However, line 254 showed higher phosphate incorporation than line 17 treated with $N_{100}P_{50}$.

Translocated P in Terminal Shoots

Translocated P, as depicted by the incorporation of phosphate into the acid-soluble fraction, was determined by assay of the terminal cm of shoots. Highest incorporation was found in seedlings grown with the same level of N and P ($N_{50}P_{50}$). However, the lowest acid-soluble phosphate transmitted to the shoot tip was in seedlings treated with 50 ppm of N and 100 ppm of P (Table 42).

There was a highly significant difference in translocated acid-soluble phosphate among lines (Table 41). Highest average value (over all treatments) was found in line 17 with lowest value in line 268. However, the difference of acid-soluble phosphate fraction in terminal shoot in line 17 and 254 was very small (Table 42).

Ranking of lines for acid-soluble phosphate in terminal shoots was the same as that for total incorporation of phosphate in all fractions in root tissue (Tables 40 and 42). It appeared that lines which absorbed more P, also translocated more P into the aerial parts. Ranking of these lines for total incorporation of

Table 42. Mean height growth (Ht), top fresh weight (Wt), and acid-soluble P translocation in one cm of terminal shoots

Lines	Traits	Treatments						
		$N_{100}P_{50}$	$N_{50}P_{50}$	$N_{10}P_1$	$N_{50}P_5$	$N_{50}P_{100}$	Mean[a]	(Rank)
				Mean Value of Three Seedlings[b]				
17	Ht (cm)	22.90	27.73	21.23	29.87	25.53	25.45	(1)
	Wt (g)	2.69	2.31	0.94	2.22	2.54	2.14	(1)
	Trans (cpm/g)	10,529	45,487	19,474	11,686	16,507	20,736	(1)
254	Ht (cm)	23.10	27.00	21.73	28.30	25.20	25.07	(2)
	Wt (g)	2.72	2.21	1.01	2.23	2.36	2.10	(2)
	Trans (cpm/g)	18,014	34,057	19,538	18,231	12,789	20,526	(2)
268	Ht (cm)	22.70	25.67	18.77	27.40	21.63	23.23	(3)
	Wt (g)	2.38	2.15	0.87	2.17	2.18	1.95	(3)
	Trans (cpm/g)	12,341	10,384	17,054	11,628	8,651	12,012	(3)
Mean[c]	Ht (cm)	22.90	26.80	20.58	28.52	24.12		
	Wt (g)	2.59	2.22	0.94	2.21	2.36		
	Trans (cpm/g)	13,628	29,976	18,689	13,689	12,649		

[a] Differences among means of height, top fresh weight, and P translocation of lines greater than 1.79, 0.23, and 2,830, respectively, are significant at 0.05 level, and greater than 1.79, 0.31, and 3,779 are significant at 0.01 level.

[b] Differences among means of height, top fresh weight, and P translocation of lines within treatments greater than 4.51, 0.59, and 7,140, respectively, are significant at 0.05 level, and greater than 6.02, 0.79, and 9,534 are significant at 0.01 level.

[c] Differences among means of height, top fresh weight, and P translocation in different treatments greater than 2.43, 0.32, and 3,845, respectively, are significant at 0.05 level, and greater than 3.20, 0.42, and 5,071 are significant at 0.01 level.

phosphate into different fractions was also similar to ranking of general combining ability of these trees used as female parents in the control-pollinated experiment for P absorption and its translocation into aerial organs (Tables 17 and 40).

Significant interaction of line x fertilizer treatment for translocated acid-soluble phosphate in 1 cm of terminal shoot was strong evidence of differential P utilization (Table 41).

Correlation of Phosphate Incorporation with Growth

Incorporation of phosphate into acid-soluble fraction in 1 cm of terminal shoot was closely correlated with height growth and top fresh weight (Fig. 7). In the upper graph of Fig. 7 the variation in translocated phosphate, based on specific activity of acid-soluble phosphate fraction in 1 cm of terminal shoot, is shown for different lines under the experimental treatments. The lower graph shows the pattern of height growth in different lines for the same fertilizer treatments. Comparison of these two graphs shows the uniformity in pattern of translocated phosphate, based on acid-soluble phosphate fraction and height growth. Except for two cases (line 17 under $N_{50}P_5$ and $N_{100}P_{50}$), the patterns of translocated phosphate and height growth were the same. Fresh weight of top was not shown here because both height growth and top fresh weight had the same ranking (Table 42).

Incorporation of phosphate into acid-soluble, nucleic acid, and phospholipid-phosphoprotein fractions in roots was closely related to height growth and top fresh weight under some of the fertilizer treatments. Although a high correlation between nutrient incorporation

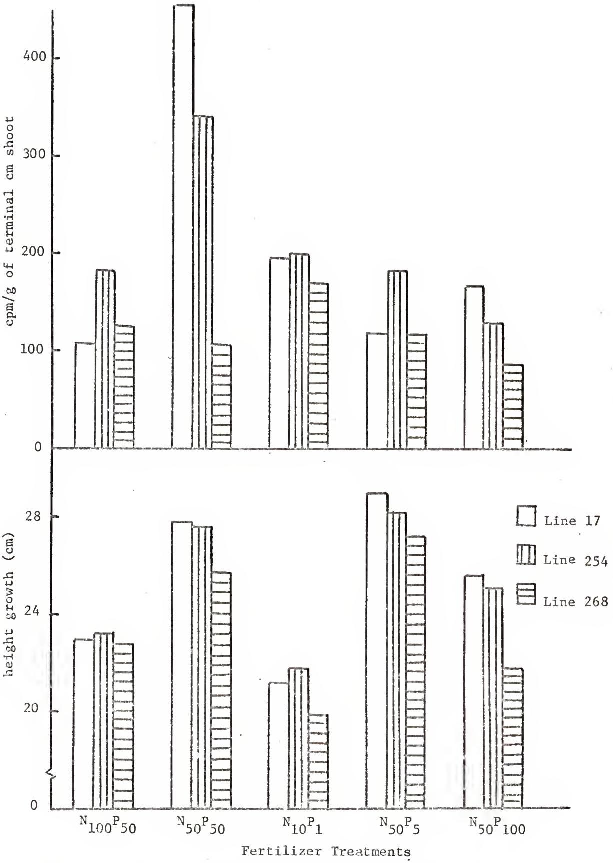

Fig. 7. Specific activity of phosphate incorporation into acid-soluble fraction in terminal cm shoots and height growth of slash pine.

and growth can be expected, the outcome of this correlation depends upon the fertilizer treatments. In this experiment, the closest relationship between phosphate incorporation and growth was obtained for seedlings grown under $N_{50}P_5$. This was found to be the best combination for growth for all 3 lines. This can be noted from the lower graph of Fig. 7 and by comparison of this graph with Figs. 8, 9, and 10.

Phenotypic correlations for incorporation of phosphate into different fractions and growth characteristics were determined on the basis of the average value of each trait over all fertilizer treatments. Individual values for each treatment were not used because, as was mentioned above, fertilizer treatments had an extremely high effect on phosphate incorporation. For example, seedlings grown on the lowest nutrient substrate ($N_{10}P_1$) showed the highest phosphate incorporation while their height growth and top fresh weight were the least among all other fertilizer treatments. This low growth was due to the deficiency of nutrients in the substrate during the growth period, while the high incorporation of phosphate into organic compounds was due to the high demand of these seedlings for P. As a result, phosphate incorporation, based on the value of each fertilizer treatment, was not used in the correlation test for growth. However, the average value of each line over all fertilizer treatments seemed to be more suitable for this purpose. Values for phenotypic correlations are given in Table 43.

The high correlation between phosphate incorporation into

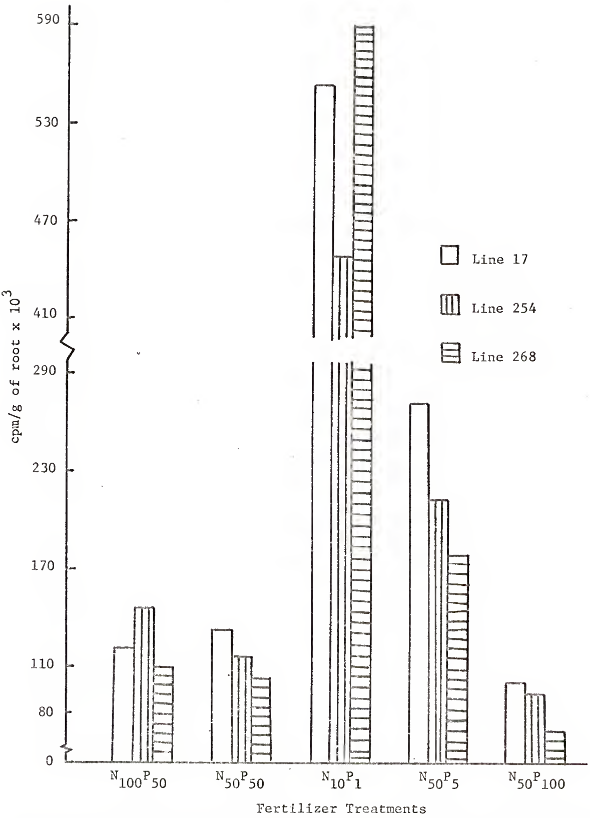

Fig. 8. Specific activity of phosphate incorporation into acid-soluble fraction in slash pine roots.

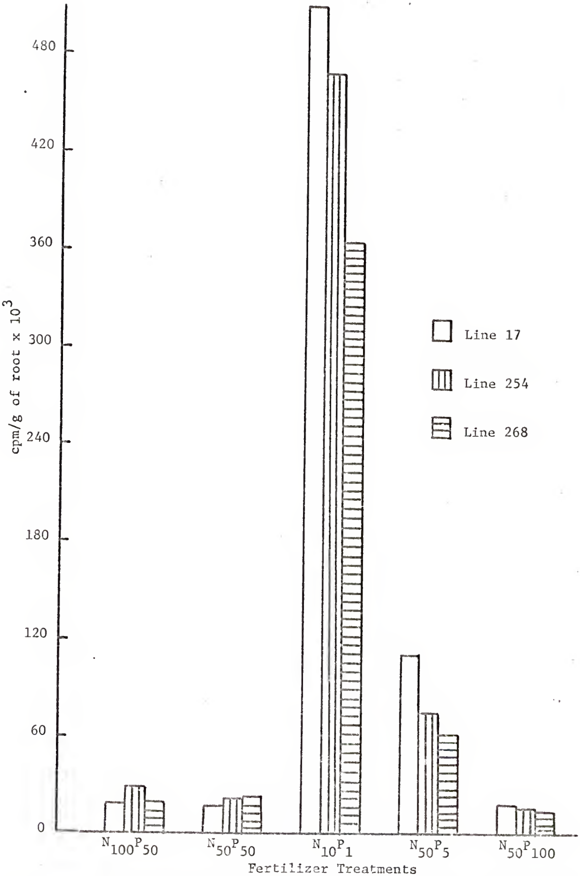

Fig. 9. Specific activity of phosphate incorporation into nucleic acid fraction in slash pine roots.

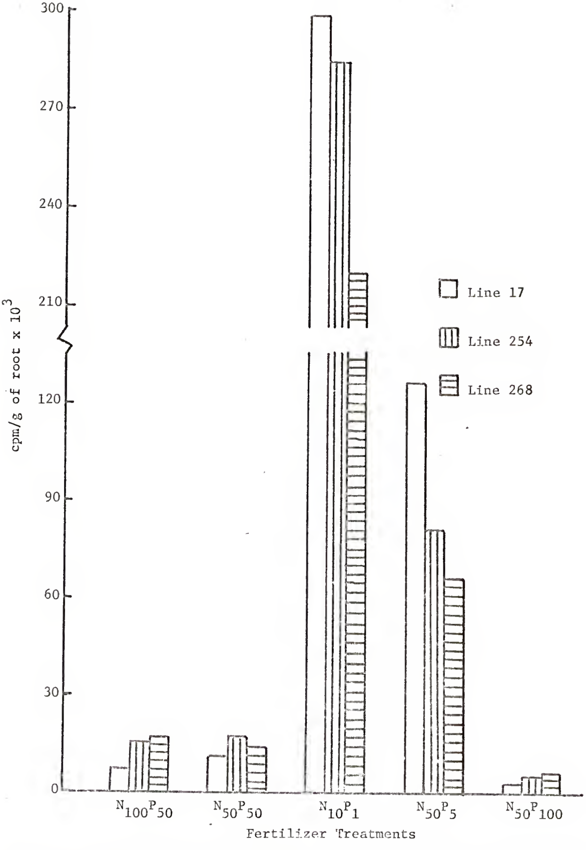

Fig. 10. Specific activity of phosphate incorporation into phospholipid-phosphoprotein fraction in slash pine roots.

Table 43. Phenotypic correlations between incorporation of P into different fractions and growth characteristics[a]

Fractions	Height Growth	Top Fresh Weight
Acid-Soluble P in Terminal Shoot	0.99^{**}	0.98^{*}
Acid-Soluble P in Root	0.66	0.69
Nucleic Acid P in Root	0.98^{*}	0.99^{**}
Phospholipid-Phosphoprotein in Root	0.98^{*}	0.99^{**}

[a] Based on average value over all fertilizer treatments.

* Significant at 0.05 level

** Significant at 0.01 level

different fractions (incorporation into acid-soluble in terminal shoots, and into nucleic acid and phospholipid-phosphoprotein in roots) and the growth characteristics was in agreement with the high genetic correlations found for N and P absorption, translocation, and the growth characteristics in the control-pollinated experiment (Tables 37 and 43).

From a physiological point of view, it appeared that the seedlings which produced more organic phosphate compounds could also produce more wood and foliage when they were grown under optimum levels of nutrients. This can possibly be a useful guide for early selection in the near future.

SUMMARY AND CONCLUSIONS

With the progress in forest tree breeding and wide interest of breeders in fertilizer application, knowledge of the genetic variation in nutrient absorption and translocation of forest tree species, along with their genetic correlations with growth characteristics becomes increasingly desirable.

The results of several experiments with pine have proved the existance of a rather strong genotype x fertilizer treatment interaction. Therefore, forest tree breeders need to distinguish fertilizer-responsive genotypes for future programs.

The selection of fertilizer-responsive genotypes on the basis of their physical response to fertilizer is not satisfactory unless the genetic property of the mechanism affecting this trait is known. Obviously, plants respond to fertilizers through absorption and translocation of nutrients and utilization of these elements for their growth.

The fertilizer-responsive genotypes can pass their characteristics on to offspring only if the mechanism of absorption, translocation and efficiency of utilization is at least partially under genetic control. Therefore, knowledge of the genetic components of variance for absorption and translocation and their correlation with growth characteristics is important in selection programs.

Accordingly, 240 control-pollinated progenies of 5 female and 5 male parents of selected slash pine were grown under N, P, NP and control treatments. Data for traits such as N and P absorption (based on total N and P in seedlings), translocation(based on total N and P in aerial organs), tissue content of each organ, and the growth characteristics were analyzed. In addition, the genetic correlations between N and P absorption and translocation and growth characteristics were determined.

Growth characteristics, such as height and diameter growth, fresh and dry weight of top, dry weight of stem and branches, dry weight of needles, and total dry weight of seedlings were all affected more by nonadditive genetic components than by additive genetic components. This was clear from the analyses of variance for the above traits in which the effects of male or female parents, except in a few cases, were not significant, while the female x male interactions were always highly significant.

Differential response to fertilizer treatments was noted for all of the growth characteristics mentioned above. Some of the crosses grew well under one fertilizer treatment, while the others performed better under other fertilizer treatments. For example, cross 262 x 196 grew taller under NP treatment, while cross 262 x 1 grew taller under P treatment.

Among the growth characteristics, root growth was the only trait which did not show any additive genetic variation. Fertilizer treatments had the greatest effect on root growth. For example, roots of seedlings grown with NP had twice the dry weight of those from seedlings without fertilizer. The effect of fertilizer was so great that it possibly masked the low additive genetic variance in the roots.

Fertilizer treatments, regardless of genetic effects and genotype x fertilizer treatment interaction, had a significant effect on growth characteristics. Except for height growth, which was maximum under P treatment, traits had highest value under NP treatment.

Fertilizer treatments also had a marked effect on the needle development of terminal shoots. Seedlings grown under NP developed needles before their full-sibs or half-sibs under other fertilizer treatments. This was followed by seedlings treated with P, control, and N, respectively. On the average, seedlings treated with P developed needles 3 days later than NP-treated seedlings. The time lag for controls was 7 days and for N-treated seedlings was as long as 20 days. The importance of this factor relates to the possible relation between the time of development of new needles and the maturity of fusiform rust spores. In practice, fertilizer treatments which result in development of succulent needle tissue at time of maximum spore release would increase seedling susceptibility.

The mean values of crosses for each trait had great fluctuation around the population mean. A male or female parent, which had the highest general combining ability, could also produce crosses with values much lower than the population mean. This would imply that a parent distinguished as superior on the basis of its general combining ability may not be superior in all cases.

Absorption and translocation of N and P and the tissue content of these elements in stem and branches and in needles were found to be partially under genetic control. However, like growth characteristics, the nonadditive genetic factor (female x male interaction) had the highest influence on these traits. The male or female parents affected the response of their progenies to fertilizer treatments. Some of the combinations of female and male parents absorbed, translocated, and utilized N and P more efficiently than the others.

There was a highly significant differential response to applied fertilizers for the above traits. A major portion of phenotypic variability in these traits was due to the genotype x fertilizer treatment interaction.

Ranking of general combining ability of parental trees for absorption of N and P and their translocation into aerial organs was the same as those for fresh and dry weight of top. It appeared that the parents which absorbed and/or translocated more N or P also produced more wood and foliage. This was an important factor because the positive response of genotypes to fertilizers was the result of their ability to absorb, translocate and utilize nutrients more effectively. It was also found that N and P content of needles was closely related to the absorption of these elements. The seedlings with higher absorption generally had higher needle content.

Heritability estimates for growth characteristics, absorption, translocation, and tissue content of N and P were determined. For each trait two estimates of heritability were made, one for general adaptability and the other for local adaptability. The heritability estimate for general adaptability is useful in estimating the genetic gain under a broad range of environments. However, the heritability based on local adaptability can be used for estimation of genetic gain when the plantation area has an environmental condition similar to that of the experimental condition.

Among the growth characteristics, height growth had a higher heritability than diameter growth, and root growth showed no heritability. Lack of heritability for root growth was due to the extremely high influence of fertilizer treatments, as discussed earlier.

Heritability estimates for N and P absorption were in order of heritability of diameter growth, and the estimates for translocation were lower than absorption. The lower heritability of translocated N and P into aerial organs was due to the effect of negative additive genetic variance of male parent for needle content. This, in turn, was influenced by the negative additive variance of male parent for needle weight. This was considered to be due to random error of sampling and/or loss of some needles from a few seedlings during the course of the experiment.

In general, the genetic components of male parents for all traits, except diameter growth, were either negative or smaller than the female genetic components. Higher genetic variation for female parents is likely not due to maternal effects; rather the lower variability among the male parents could have been due to random error of selection. The random error of selection could have been minimized by selecting a larger sample from the population.

The heritability estimates under general adaptability presented in this study could have been much higher if less diverse soil nutrients had been used. This is inferred from the high heritability estimates determined under local adaptability. Accordingly, estimates of additive genetic variance of different traits reported here are considered to have been minimized by the high effects of genotype x fertilizer treatment interaction components. On the other hand, the interaction components have been maximized due to the high diversity of soil nutrients.

Genetic correlations between N and P absorption, translocation, and needle content, and growth characteristics were calculated. Growth characteristics other than diameter growth were found to be genetically correlated with N and P absorption, translocation, or needle content. Similarly, N and P translocation and needle content were genetically correlated with absorption. In contrast, there were no genetic correlations between N and P absorption, translocation, or needle content and diameter growth. Also, height growth and diameter growth were not genetically correlated.

In a supplementary experiment using ^{33}P and open-pollinated progenies of the female parents used in the control-pollinated experiment, the incorporation of the phosphate into acid-soluble, nucleic acid, and phospholipid-phosphoprotein fractions was studied. Data showed that (a) incorporation of phosphate into the above fractions was highly dependent on the rate of N and P in substrate, (b) incorporation of phosphate into different fractions in seedlings treated with 50 ppm of N and 5 ppm of P (optimum levels of N and P in the experiment) was highly associated with height growth and top fresh weight, (c) there were significant correlations between incorporation of phosphate into nucleic acid and phospholipid-phosphoprotein fractions in roots and growth characteristics, when average values for incorporation over all fertilizer treatments were used, and (d) there were significant correlations between translocated P, based on acid-soluble phosphate in terminal cm shoots, and growth characteristics. Here growth characteristics were shoot height and top fresh weight.

The high genetic correlations between absorption, incorporation, and/or translocation and growth characteristics, found in both experiments, may suggest the possibility of selection of fertilizer-responsive genotypes on the basis of absorption, incorporation, and/or translocation of nutrients. This may be more effective than direct selection based on physical observation. In addition, the presence of high genetic correlation may be considered as a useful tool in selection of fertilizer-responsive genotypes at an early stage of development (seedling stage) on the basis of absorption, incorporation and/or translocation of nutrients. This procedure can be used if more reliable data concerning genetic correlations between growth characteristics at different stages of maturity in slash pine become available.

From the foregoing discussion it can be concluded that:

1. Absorption of N and P and their translocation into aerial organs in slash pine is partially under genetic control and therefore can be transmitted from parents to offspring.

However, nonadditive genetic effects have a much greater influence than additive genetic effects.

2. There is a highly significant differential absorption and translocation of N and P with respect to fertilizer treatments. Some combinations of male and female parents may absorb and translocate nutrients more effectively under one nutrient regime, while the others may do better under another nutrient regime.
3. Absorption, translocation, and needle content of N and P are genetically correlated with growth characteristics, based on top and total dry weight, stem and branches dry weight, top fresh weight, and height growth of seedlings. It also appeared that the N and P content of needles can be used as an index to absorption and/or translocation.
4. Selection of fertilizer-responsive individuals or families of slash pine can be carried out on the basis of absorption and/or translocation of nutrients, or on the basis of incorporation of nutrients into organic compounds under an optimum growth substrate. However, in the case of height growth, the lower heritability estimates of absorption and/or translocation do not justify selection on the basis of these traits. In this case, absorption and/or translocation can be used as growth-determining factors for early selection.
5. When a progeny test has been carried out under some fertilizer practice, the magnitude of genotype x fertilizer

treatment interaction must be considered in estimation of genetic gain in the next generation.

It should be noted that soil is a major part of plant environment and affects the outcome of experiments to a great extent. Accordingly, the fact that a nutrient deficient soil, especially in P content, was used as a reference medium in this study should not be overlooked. The results of this experiment are more applicable to areas with nutrient deficient soils, and need more consideration for other soils.

APPLICATION OF RESULTS TO FOREST TREE BREEDING

The high heritability estimates for growth characteristics under local adaptability suggest that a high genetic gain can be achieved if selection is based on general combining ability for areas uniform in soil characteristics. One may develop genotypes suitable for nutrient deficient soils and responsive to some fertilizer. These genotypes can be preserved in seed orchards to be used for plantations in specific areas. It should be noted, however, that with the heritability values under general adaptability, estimated in this experiment, some improvement will be achieved if breeding is carried out on the basis of general combining ability for a broader range of environment. In this case, genetic gain can be increased if selection is made for trees capable not only of producing open-pollinated progenies superior to others in the population, but also exhibiting a minimum variation among their half-sib progenies.

Moreover, maximum genetic gain can be achieved if selection is based on specific combining ability rather than general combining ability. Fertilizer-responsive genotypes can be selected for seed orchards on the basis of their specific combining abilities under certain fertilizers. However, the practicability of doing so is not quite clear at this stage. Capitalization on specific combining ability may require control-pollination or use of separate orchards for different pairs of clones. While the problem of so-called "narrow gene pool" can be overcome by maintaining several seed orchards, each with different genotypes, economical justification is a matter of concern which should be weighed against the increase in expected genetic gain.

Fertilizer-responsive genotypes may be selected in an early stage of development on the basis of their ability for nutrient absorption, incorporation, and/or translocation. In this case, assumption is made that these traits are less subject to fluctuation during the early stage of development than physical responses. A high genetic correlation between growth at early stage of development and that at maturity is essential for this procedure.

APPENDIX

Table A-1. Concentration of N in roots in percent dry weight[a]

		MALE PARENTS					
FEMALE PARENTS	Treatments	1	5	12	98	196	Mean
17	N	1.434	1.391	1.586	1.377		1.447
	P	0.464	0.552	0.551	0.498		0.516
	NP	1.053	1.047	1.004	0.918		1.006
	Control	0.861	0.686	0.999	0.861		0.852
268	N	1.252	1.008	0.995		1.130	1.096
	P	0.598	0.620	0.668		0.496	0.596
	NP	0.911	1.151	0.866		1.107	1.009
	Control	0.955	0.828	1.008		0.641	0.858
254	N	1.145	1.401		1.203	1.135	1.221
	P	0.487	0.535		0.530	0.623	0.544
	NP	1.046	1.295		0.936	1.059	1.084
	Control	0.746	0.955		0.822	0.774	0.824
262	N	1.457		1.133	1.291	1.079	1.240
	P	0.443		0.555	0.474	0.507	0.495
	NP	1.057		1.034	1.072	0.931	1.024
	Control	0.648		0.590	0.620	0.875	0.683
87	N		1.200	1.244	1.407	1.346	1.299
	P		0.593	0.499	0.550	0.577	0.555
	NP		1.185	1.018	1.006	1.022	1.058
	Control		0.688	0.760	0.775	0.892	0.779
Mean	N	1.322	1.250	1.240	1.320	1.173	
	P	0.498	0.575	0.568	0.513	0.551	
	NP	1.017	1.170	0.981	0.983	1.030	
	Control	0.803	0.789	0.839	0.770	0.796	

[a] Values are mean of 3 seedlings.

Table A-2. Concentration of N in stem and branches in percent dry weight[a]

		MALE PARENTS					
FEMALE PARENTS	Treatments	1	5	12	98	196	Mean
17	N	0.736	0.722	0.711	0.708		0.719
	P	0.300	0.330	0.372	0.334		0.334
	NP	0.839	0.852	0.873	0.911		0.869
	Control	0.450	0.404	0.499	0.393		0.437
268	N	0.941	0.733	0.698		0.777	0.787
	P	0.333	0.333	0.317		0.293	0.319
	NP	1.019	1.092	0.988		1.089	1.047
	Control	0.494	0.504	0.511		0.373	0.471
254	N	0.639	0.720		0.691	0.588	0.660
	P	0.283	0.317		0.269	0.352	0.305
	NP	0.877	0.911		0.847	0.815	0.863
	Control	0.403	0.445		0.395	0.408	0.413
262	N	0.625		0.645	0.792	0.489	0.638
	P	0.283		0.234	0.336	0.273	0.282
	NP	1.130		1.102	1.149	0.863	1.061
	Control	0.351		0.408	0.412	0.449	0.405
87	N		0.616	0.633	0.553	0.845	0.662
	P		0.405	0.262	0.303	0.263	0.308
	NP		0.805	0.866	0.942	0.824	0.859
	Control		0.384	0.450	0.390	0.370	0.399
Mean	N	0.735	0.698	0.672	0.686	0.675	
	P	0.300	0.346	0.296	0.311	0.295	
	NP	0.966	0.915	0.957	0.962	0.898	
	Control	0.425	0.434	0.467	0.398	0.400	

[a] Values are mean of 3 seedlings.

Table A-3. Concentration of N in needles in percent dry weight[a]

			MALE PARENTS				
FEMALE PARENTS	Treatments	1	5	12	98	196	Mean
17	N	3.428	3.351	3.113	3.159		3.263
	P	0.944	0.920	0.941	0.873		0.920
	NP	1.689	1.584	1.682	1.478		1.608
	Control	1.965	1.722	2.657	2.056		2.100
268	N	2.943	3.039	2.780		2.609	2.843
	P	1.132	1.018	1.056		0.852	1.015
	NP	1.717	1.890	1.517		1.809	1.733
	Control	2.066	2.262	1.939		1.392	1.915
254	N	2.482	2.790		2.639	2.692	2.651
	P	0.762	0.979		0.970	0.921	0.908
	NP	1.402	1.490		1.390	1.553	1.459
	Control	1.581	1.699		1.377	1.609	1.567
262	N	2.745		3.071	3.092	3.148	3.014
	P	0.853		0.964	1.023	1.066	0.977
	NP	1.719		2.130	1.732	1.647	1.807
	Control	1.683		1.331	1.608	2.128	1.688
87	N		3.152	3.305	3.272	2.993	3.181
	P		0.997	0.920	0.947	1.146	1.003
	NP		1.565	1.560	1.473	1.698	1.574
	Control		1.490	1.866	1.876	2.017	1.812
Mean	N	2.900	3.083	3.067	3.041	2.861	
	P	0.923	0.979	0.970	0.953	0.996	
	NP	1.632	1.632	1.722	1.518	1.677	
	Control	1.824	1.793	1.949	1.730	1.787	

[a] Values are mean of 3 seedlings.

Table A-4. Concentration of P in roots in percent dry weight[a]

		MALE PARENTS					
FEMALE PARENTS	Treatments	1	5	12	98	196	Mean
17	N	0.032	0.030	0.032	0.031		0.031
	P	0.102	0.087	0.096	0.084		0.092
	NP	0.069	0.073	0.083	0.078		0.076
	Control	0.036	0.031	0.034	0.028		0.032
268	N	0.031	0.031	0.032		0.029	0.031
	P	0.099	0.099	0.095		0.104	0.099
	NP	0.100	0.094	0.092		0.095	0.095
	Control	0.035	0.034	0.036		0.028	0.033
254	N	0.029	0.030		0.029	0.030	0.030
	P	0.095	0.113		0.093	0.100	0.100
	NP	0.085	0.076		0.084	0.095	0.085
	Control	0.032	0.039		0.035	0.032	0.035
262	N	0.034		0.027	0.037	0.033	0.033
	P	0.096		0.100	0.094	0.105	0.099
	NP	0.087		0.073	0.072	0.083	0.079
	Control	0.035		0.031	0.032	0.034	0.033
87	N		0.032	0.034	0.031	0.037	0.034
	P		0.107	0.102	0.094	0.107	0.104
	NP		0.083	0.080	0.087	0.087	0.084
	Control		0.032	0.035	0.036	0.039	0.036
Mean	N	0.032	0.031	0.031	0.032	0.032	
	P	0.098	0.102	0.098	0.091	0.104	
	NP	0.085	0.082	0.082	0.080	0.090	
	Control	0.035	0.034	0.034	0.033	0.033	

[a] Values are mean of 3 seedlings.

Table A-5. Concentration of P in stem and branches in percent dry weight[a]

		MALE PARENTS					
FEMALE PARENTS	Treatments	1	5	12	98	196	Mean
17	N	0.019	0.021	0.020	0.018		0.020
	P	0.085	0.091	0.088	0.087		0.088
	NP	0.080	0.081	0.078	0.079		0.080
	Control	0.021	0.018	0.023	0.017		0.020
268	N	0.019	0.020	0.021		0.022	0.021
	P	0.080	0.072	0.075		0.060	0.072
	NP	0.104	0.087	0.092		0.098	0.095
	Control	0.022	0.020	0.019		0.017	0.020
254	N	0.020	0.018		0.020	0.017	0.019
	P	0.069	0.082		0.071	0.069	0.073
	NP	0.096	0.070		0.102	0.080	0.087
	Control	0.020	0.019		0.018	0.017	0.019
262	N	0.020		0.018	0.018	0.019	0.019
	P	0.080		0.069	0.080	0.074	0.076
	NP	0.105		0.086	0.072	0.080	0.086
	Control	0.019		0.020	0.018	0.017	0.019
87	N		0.022	0.018	0.018	0.019	0.019
	P		0.072	0.079	0.072	0.066	0.072
	NP		0.069	0.065	0.088	0.079	0.075
	Control		0.018	0.020	0.019	0.020	0.019
Mean	N	0.020	0.020	0.019	0.019	0.019	
	P	0.079	0.079	0.078	0.078	0.067	
	NP	0.096	0.077	0.080	0.085	0.084	
	Control	0.020	0.019	0.021	0.018	0.018	

[a] Values are mean of 3 seedlings

Table A-6. Concentration of P in needles in percent dry weight[a]

		MALE PARENTS					
FEMALE PARENTS	Treatments	1	5	12	98	196	Mean
17	N	0.036	0.036	0.037	0.029		0.035
	P	0.111	0.090	0.102	0.087		0.097
	NP	0.105	0.097	0.103	0.104		0.102
	Control	0.038	0.040	0.034	0.034		0.036
268	N	0.045	0.046	0.041		0.039	0.043
	P	0.100	0.096	0.108		0.083	0.097
	NP	0.117	0.112	0.123		0.124	0.119
	Control	0.041	0.039	0.041		0.039	0.040
254	N	0.037	0.037		0.038	0.035	0.037
	P	0.086	0.099		0.094	0.087	0.091
	NP	0.106	0.114		0.111	0.106	0.109
	Control	0.041	0.036		0.041	0.038	0.039
262	N	0.034		0.039	0.035	0.040	0.037
	P	0.088		0.089	0.099	0.097	0.093
	NP	0.120		0.121	0.108	0.110	0.115
	Control	0.042		0.041	0.039	0.037	0.040
87	N		0.032	0.033	0.032	0.040	0.034
	P		0.093	0.102	0.094	0.103	0.098
	NP		0.097	0.108	0.109	0.118	0.108
	Control		0.036	0.034	0.032	0.035	0.034
Mean	N	0.038	0.038	0.038	0.034	0.039	
	P	0.096	0.095	0.100	0.094	0.093	
	NP	0.112	0.105	0.114	0.108	0.115	
	Control	0.041	0.038	0.038	0.037	0.037	

[a] Values are mean of 3 seedlings.

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BIOGRAPHICAL SKETCH

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Sirous Tamaddoni Jahromi is married to the former Paula Alice Longnecker. He is a member of Xi Sigma Pi and Sigma Xi.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Ray E. Goddard

Ray E. Goddard, Chairman
Associate Professor of Forestry and Agronomy

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Dean of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

June, 1971

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